

# Land Caenogastropods of Mounts Mahermana, Ilapiry, and Vasiha, Southeastern Madagascar, with Conservation Statuses of 17 Species of *Boucardicus*

KENNETH C. EMBERTON

Molluscan Biodiversity Institute, 110 Old Airport Road, Concord, North Carolina 28025, USA

AND

TIMOTHY A. PEARCE\*

Delaware Museum of Natural History, Box 3937, Wilmington, Delaware 19807-0937, USA

**Abstract.** Quantitative, replicated altitudinal transects on the three mountains yielded 25 caenogastropod species in six genera in four families. *Madecataulus* Fischer-Piette & Bedoucha, 1965, is synonymized under *Boucardicus* Fischer-Piette & Bedoucha, 1965. Presence is noted of the three large species *Hainesia crocea* (Sowerby, 1847), *Tropidophora* sp. 1, and *T.* sp. 2. Descriptions are given of the small species *Boucardicus albocinctus* (E. A. Smith, 1893); *B. antiquus* sp. nov.; *B. carylae* sp. nov.; *B. culminans* (Fischer-Piette, Blanc, Blanc & Salvat, 1993); *B. curvifolius* sp. nov.; *B. delicatus* sp. nov.; *B. divei* Fischer-Piette, Blanc, Blanc & Salvat, 1993; *B. esetrae* sp. nov.; *B. fidimananai* sp. nov.; *B. fortistriatus* sp. nov.; *B. magnilobatus* sp. nov.; *B. mahermanae* sp. nov.; *B. rakotoarisoni* sp. nov.; *B. randalanai* sp. nov.; *B. simplex* sp. nov.; *B. tridentatus* sp. nov.; *B. victorhernandezi* Emberton, 1998; *Cyathopoma randalana* sp. nov.; *Malarinia calcopercula* Emberton, 1994; *Tropidophora (Ligatella) vallorzi* Fischer-Piette, Blanc, Blanc & Salvat, 1993; *Omphalotropis vohimenae* sp. nov.; and *O. costulata* sp. nov.

Distributional data were available that allowed evaluation of each of the 17 *Boucardicus* species for its conservation status, applying the latest IUCN criteria. Four species are proposed as Critically Endangered, 11 as Endangered, and two as Vulnerable.

## INTRODUCTION

Recent quantitative sampling of altitudinal transects on Mounts Mahermana, Ilapiry, and Vasiha in southeastern Madagascar yielded 88 species of land snails and slugs (Emberton et al., 1996, 1999; Emberton, 1997). Of these, 81 species are small ("micro") land snails (< 5 mm in greatest dimension at any collected life stage). Analyses of the distributions of 80 of these species have shown that (a) the best sampling strategy for Madagascar-rain-forest snails is timed searching for micro-snails, while incidentally collecting macro-snails and litter-plus-soil for later picking of the 5.5–1.2 mm and the 1.2–0.85 mm, dry-sieved fractions (Emberton et al., 1996); (b) total land-snail diversity is significantly higher in the unprotected Vohimena Mountain Chain than in the protected Anosy Mountain Chain (Emberton et al., 1999); (c) the Vohimena Chain's greater richness occurs in four of the eight major groups of land snails (charopids; *Microcystis* Beck, 1837; *Kalidos* Gude, 1911; and non-*Boucardicus* "prosobranchs" [caenogastropods]), and does not exist for the other four groups (*Boucardicus* Fischer-Piette &

Bedoucha, 1965; streptaxids; *Sitala* H. Adams, 1865; and other pulmonates) (Emberton, 1997); (d) there is evidence that lowlands are richer than highlands in endemic and rare species (Emberton, 1997); and the small land snails (e) are sensitive ecological indicators of mild forest degradation from selective cutting or nearby slash-and-burn, and (f) do not seem to compete with congeners via shell size (Pearce & Emberton, unpublished).

All of those conclusions were based on undocumented morphospecies. This paper is the first in a series of four papers that identify and describe the species. This paper treats the Mahermana-Ilapiry-Vasiha caenogastropods.

In the interests of conservation in Madagascar, it is important to provide as much Red-List data (IUCN, 1996) as possible. In this paper, we evaluate the conservation statuses of the 17 *Boucardicus* species described herein.

## MATERIALS AND METHODS

Collecting methods have been detailed by Emberton et al. (1996). Sixteen stations were collected and numbered in the "Tol" series (for Tolagnaro = Fort Dauphin, the nearest city). These stations have been mapped by Emberton et al. (1996, 1999) and in Emberton (1997). To

\* To whom reprint requests should be sent.

shorten the taxonomic descriptions, stations are described briefly below. Station numbers are in the series of the Molluscan Biodiversity Institute (MBI). All stations were restricted to primary forest that had no more than limited selective cutting. Ecological data are given by Emberton (1997:table 1). All stations are in Madagascar: Tuléar Province. Mount Mahermana (Vohimena Chain) is north-east of the village of Esetra, Ilapiry (Vohimena Chain) is west of Mahialambo, and Vasiha (Anosy Chain) is west of Malio. Latitude and longitude are given in degrees, minutes, and seconds.

MBI 373 (= Tol-1). Summit of Mt. Mahermana, 340 m, 24°26'12"S, 47°13'13"E.

MBI 374 (= Tol-2). Slope of Mt. Mahermana, 300 m, 24°26'17"S, 47°13'10"E.

MBI 375 (= Tol-3). Slope of Mt. Mahermana, 200 m, 24°26'15"S, 47°13'04"E.

MBI 376 (= Tol-4). Valley on Mt. Mahermana, 100 m, 24°26'22"S, 47°12'41"E.

MBI 377 (= Tol-5). Summit of Mt. Ilapiry, 540 m, 24°51'40"S, 47°00'20"E.

MBI 378 (= Tol-6). Ridge on Mt. Ilapiry, 500 m, 24°51'33"S, 47°00'27"E.

MBI 379 (= Tol-7). Ridge, valley, and slope on Mt. Ilapiry, 400 m, 24°51'27"S, 47°00'38"E.

MBI 380 (= Tol-8). Slope of Mt. Ilapiry, 300 m, 24°51'36"S, 47°00'40"E.

MBI 381 (= Tol-9). Slope of Mt. Ilapiry, 200 m, 24°51'39"S, 47°00'46"E.

MBI 382 (= Tol-10). Lower summit of Mt. Vasiha, 860 m, 24°55'18"S, 46°44'19"E.

MBI 383 (= Tol-11). Slope of Mt. Vasiha, 700 m, 24°55'23"S, 46°44'27"E.

MBI 384 (= Tol-12). Slope of Mt. Vasiha, 500 m, 24°55'19"S, 46°44'45"E.

MBI 385 (= Tol-13). Valley on Mt. Vasiha, 400 m, 24°55'25"S, 46°44'45"E.

MBI 386 (= Tol-14). Slope of Mt. Vasiha, 300 m, 24°55'37"S, 46°44'49"E.

MBI 387 (= Tol-15). Slope of Mt. Vasiha, 200 m, 24°56'13"S, 46°45'13"E.

MBI 388 (= Tol-16). Slope of Mt. Vasiha, 100 m, 24°56'20"S, 46°46'07"E.

MBI 389 (= Tol-3-4). Incidental collecting between Tol-3 and Tol-4.

MBI 390 (= Tol-1-2). Incidental collecting between Tol-1 and Tol-2.

MBI 391 (= Tol-sub-5). Incidental collecting below summit of Mt. Ilapiry, Tol-5.

MBI 392 (= Tol-7-9). Incidental collecting between Tol-7 and Tol-9.

Species identifications and comparisons were made using Fischer-Piette et al. (1993) and Emberton (1994, 1998). All caenogastropod species were identified, but, as Madagascar's large caenogastropod species are either fairly well known (Fischer-Piette et al., 1993) or—in the

case of large *Tropidophora*—in taxonomic chaos (Emberton, 1995), descriptions were prepared only for the small species.

For each small species, the holotype or a representative shell was photographed in apertural, basal, and side views at either  $\times 10$ ,  $\times 16$ ,  $\times 25$ , or  $\times 40$  magnification, and in apical view at  $\times 40$  magnification. Additional specimens were photographed as needed to illustrate shell variation or ontogeny.

Fifty-eight shell characters (Table 1, Figure 1) were measured, or measured and calculated, or scored from the photographs or from the shells themselves.

At least one adult male or female anatomy was available for 12 (71%) of the *Boucardicus* species. From each of these species, one to three reproductive systems were removed and illustrated by photographs and/or camera-lucida drawings as they were turned and progressively dissected to expose characters in the penis and FPSC (fertilization pouch-seminal receptacle complex). Only the penis and FPSC were examined because of time constraints and because these two organs seemed most likely to contain informative characters, based on previous experience. Seventeen reproductive-anatomical characters (Table 1, Figures 26–31) were taken from the drawings or from the dissections themselves.

Character matrices were prepared (available from K.C.E. on request) and were used to code character-state data into the DELTA system (Partridge et al., 1993; Dallwitz et al., 1993), which was then used to generate natural-language species descriptions. Computer-assisted taxonomic descriptions and keys have been developed over the years by a number of approaches (e.g., Pankhurst, 1975; Watson et al., 1986), arguably culminating in the DELTA system (Partridge et al., 1993; Dallwitz et al., 1993). DELTA is "a flexible data-coding format for taxonomic descriptions, and an associated set of programs for producing and typesetting natural-language descriptions and keys, for interactive identification and information retrieval, and for conversion of data to formats required for phylogenetic and phenetic analysis" (Partridge et al., 1993).

For each *Boucardicus* species, conservation status was evaluated using the latest categories and criteria of the International Union for the Conservation of Nature (IUCN, 1996). Ranges were estimated from distribution data in Emberton (in press). Rainforest extent and decline were assessed using Green & Sussman (1990), Sussman et al. (1994), and the most recently available topographic maps.

## INFERENCE OF HOMOLOGIES

Interpretations of shell homologies were straightforward. Penis width was ruled out as a character, because during mating it can be drastically swollen (Figure 38 versus Figure 37). In the FPSC (fertilization pouch-seminal re-



Table 1

Shell and reproductive characters used in descriptions.

## SHELL

1. Diameter (0.1 mm)
2. Height (0.1 mm)
3. Height/Diameter (0.1)
4. Spire angle (degrees)
5. Whorl periphery shape (round, angular, keeled)
6. Whorl shoulder shape (round, flat)
7. Aperture width parallel to parietal callus (% diameter)
8. Aperture height (perpendicular to parietal callus)/width (0.01)
9. Columellar plica (yes, no)
10. Aperture-plane inclination upward from rotational axis (5 degrees)
11. Apertural anal notch depth (% apertural width)
12. Baso-columellar denticle size (% apertural width)
13. Baso-columellar denticle depth (0.05 whorl)
14. Basal denticle size (% apertural width)
15. Basal denticle depth (0.05 whorl)
16. Upper palatal denticle size (% apertural width)
17. Upper palatal denticle depth (0.05 whorl)
18. Peristome angle of greatest dimension outward from rotational axis (5 degrees)
19. Peristome greater dimension/aperture width in same direction (0.01)
20. Peristome greatest dimension/lesser, perpendicular dimension (0.01)
21. Peristome baso-palatal indentation (% basal peristome width)
22. Peristome upper curl forward extension (% upper peristome width)
23. Inner, second peristome (none, projecting up to 0.01 whorl, projecting up to 0.05 whorl)
24. Umbilicus size pre-constriction (% diameter)
25. Umbilicus size total (% diameter)
26. Whorl number (0.1)
27. Embryonic whorl number (0.1)
28. Embryonic whorl sculpture
29. First whorl diameter (0.01 mm)
30. First three whorls diameter (0.01 mm)
31. Penult-whorl complete spiral grooves depth (0.01 mm)
32. Penult-whorl complete spiral grooves number between sutures
33. Penult-whorl spiral ridges height (0.01 mm)
34. Penult-whorl spiral ridges number between sutures
35. Penult-whorl spiral grooves or ridges waviness (none, slight, moderate)
36. Penult-whorl transverse ribs height (0.01 mm)
37. Penult-whorl transverse ribs number in last 0.1 whorl
38. Penult-whorl herringbone sculpture (Figures 4, 10) number in last 0.1 whorl
39. Penult-whorl honeycomb sculpture (Figure 19) number per 0.1 whorl
40. Penult-whorl short spiral grooves number between sutures
41. Penult-whorl short spiral grooves length (0.01 mm)
42. Penult-whorl spiral lines of punctae number between sutures
43. Penult-whorl spiral lines of punctae number per 0.1 whorl
44. Pre-apertural constriction distance from aperture (0.1 whorl)
45. Pre-apertural constriction (% whorl diameter constriction)
46. Pre-constriction diminution of sculpture (%)

Table 1

Continued.

47. Post-constriction immediate percent diameter swelling (%)
48. Post-constriction secondary constriction (yes, no)
49. Post-secondary constriction swelling (% diameter of first constriction)
50. Pre-apertural transverse ribs height (0.01 mm)
51. Pre-apertural transverse ribs procumbancy angle
52. Pre-apertural transverse ribs number per 0.1 whorl
53. Color general
54. Color apex
55. Spiral color band number
56. Spiral color band color
57. Preapertural constriction color
58. Peristome color (excluding periostracum)

## PENIS

59. Length (0.1 mm)
60. Length/ shell diameter (0.1)
61. Terminal papilla-ejaculatory pore position (dorsal, central, ventral)
62. Dorsal papilla-ejaculatory pore position (terminal, subterminal)
63. Papilla protrusion (none, slight, strong)
64. Papilla direction (anterior, posterior)
65. Swelling at tip of penis: swelling width/pre-swelling width (0.1)
66. Gland (present, absent)
67. Gland length/pre-swelling penial width (0.1)
68. Gland proximal-distal position: distance from base of penis to midpoint of gland/penial length (0.1)
69. Gland dorsal-ventral attachment position (dorsal, ventral)
70. Gland free-lobe direction (left, right)

## FPSC (FERTILIZATION POUCH-SEMINAL RECEPTACLE COMPLEX)

71. Base (present, absent)
72. Base shape
73. Base ducted gland (present, absent)
74. Body-interior muscular funnel (present, absent)
75. Body-and-tube shape

ceptacle) great morphological diversity (Figures 27–31, 55–68) called for some judgment. Internal structures of two disparate morphologies (Figures 53, 54) led to the hypothesis of three distinct regions of the *Boucardicus* FPSC (Figures 27–31). The *base* appears to be lined with glandular tissue, and it may or may not have additional glandular lobes, or an appendage, or a ducted or ductless gland; the shape of the base varies from globular to thin and elongate; *Cyathopoma* seems to lack a base. The FPSC *body* seems to be a muscular tube that may or may not contain a muscular, funnel-shaped organ (Figure 54). Apically (i.e., proximally), the body grades into a thinner-walled *tube*; the gradation can be abrupt or gradual.

## SYSTEMATICS

Higher classification follows Ponder & Lindberg (1997) and Vaught (1989). Type materials are placed in the Unit-

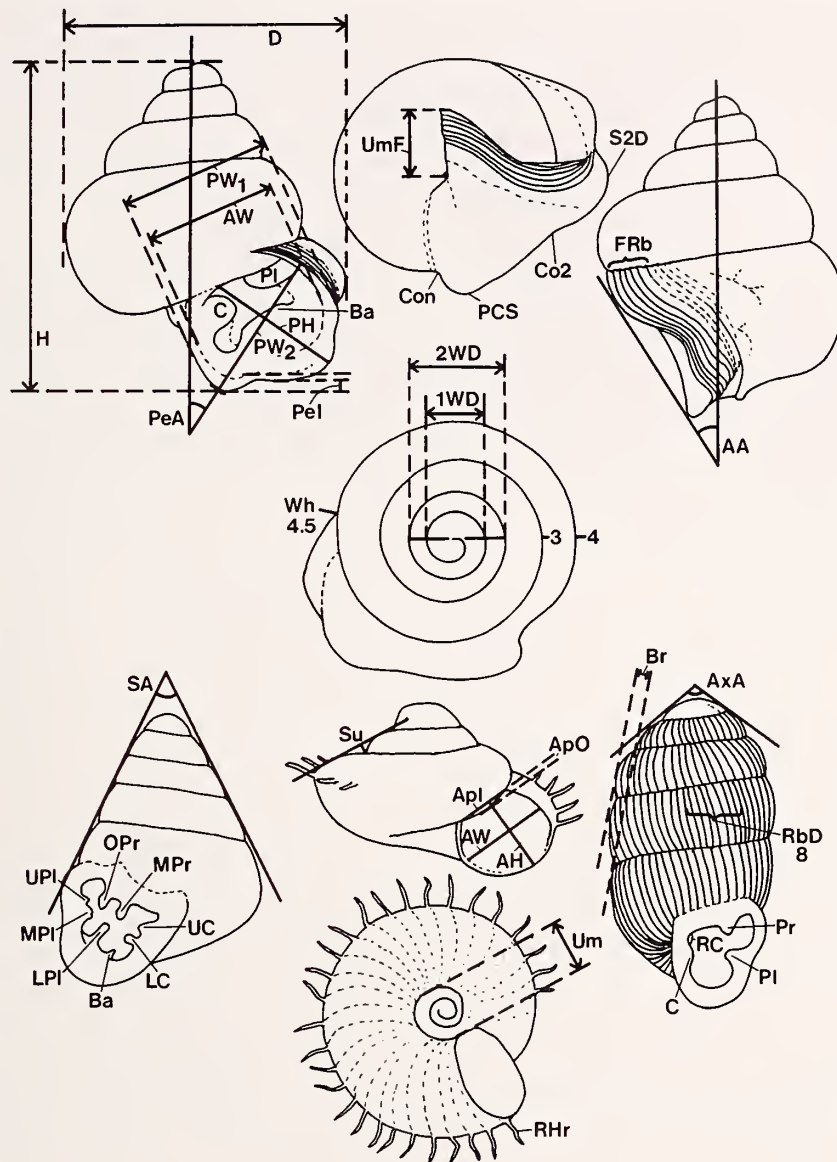


Figure 1

Some of the shell features measured, scored, and used in calculating characters (Table 1), shown on *Boucardicus* (above) and some pulmonates (below). 1WD, first whorl diameter; 2WD, first two whorls diameter; AA, angle at which apertural plane is inclined from rotational axis; AH, aperture height (inside dimension measured to and perpendicular to a line between columellar and upper peristome insertions); ApI, distance between the columellar and upper peristome insertions; ApO, amount of aperture occupied by previous whorl; AW, aperture width (inside dimension measured parallel to a line between the columellar and upper peristome insertions); AxA, apex angle; Ba, basal denticle; Br, barreling (outward departure from a straight line of a tangent to the whorls between  $n-0.5$  and about the second whorl); C, columellar denticle; Co2, second body whorl constriction; Con, body whorl constriction; D, shell diameter; FRb, final ribs near body whorl aperture; H, shell height; LC, lower columellar denticle; LPI, lower palatal denticle; MPI, middle palatal denticle; MPr, middle parietal denticle; OPr, outer parietal denticle; PCS, post-constrictional body whorl swelling; PeA, angle from greatest width of aperture plus peristome to rotational axis; PeI, peristome baso-palatal indentation (expressed as percent of basal peristome width, i.e., to the unlabelled line above it in the figure); PH, aperture plus peristome greatest height as measured perpendicular to greatest width line; PI, palatal denticle; Pr, parietal denticle; PW1, aperture plus peristome width (measured parallel to aperture width); PW2, aperture plus peristome greatest width (measured on *Boucardicus*, parallel to or within 40 degrees of parietal-callus line); RbD, transverse rib density (number in estimated tenth of whorl); RC, recessed columellar denticle; RHr, rib hairs; S2D, swelling after second body whorl constriction; SA, spire angle; Su, suture depth one half whorl from aperture; UC, upper columellar denticle; Um, umbilicus size before any change in body whorl growth direction; UmF, final umbilicus total size; UPI, upper palatal denticle; Wh, whorl number.



ed States National Museum, Washington, D.C. (USNM); temporarily in the Molluscan Biodiversity Institute (MBI), all of whose collections will revert in the near future to USNM; and in the Australian Museum, Sydney (AMS); the Muséum National d'Histoire Naturelle, Paris (MNHN); and the Academy of Natural Sciences of Philadelphia (ANSP). MBI catalog numbers consist of station number (see Methods section), reference number of the species, D (dry) or A (alcohol-preserved), and when appropriate H (holotype) or P (paratype) or R (representative).

### Class GASTROPODA

### Clade CAENOGASTROPODA

### Superfamily CYCLOPHOROIDEA

### Family CYCLOPHORIDAE

### Genus *Boucardicus* Fischer-Piette & Bedoucha, 1965

New Synonym: *Madecataulus* Fischer-Piette & Bedoucha, 1965 (type species *Madecataulus goudoti* Fischer-Piette & Bedoucha, 1965). The operculum and preapertural constriction and swelling of *Madecataulus* are virtually identical to those of *Boucardicus* (Emberton, 1994). The high spire seems insufficient to define a distinct genus.

### *Boucardicus esetrae* Emberton & Pearce, sp. nov.

(Figures 2, 29, 33, 55)

*Boucardicus* n. sp. 19, Emberton, 1996:735.

*Boucardicus* sp. 1, Emberton et al., 1996:210. Emberton, 1997:1146, 1149. Emberton et al., 1999:table 2.

**Holotype:** USNM 860776 (ex MBI 382.01DH, adult shell).

**Paratypes:** MBI 374.05DP (1 adult, 1 juvenile), MBI 377.05DP (1 ad, 1 juv), MBI 378.07DP (1 juv), MBI 378.07AP (1 juv), MBI 380.05DP (1 ad), MBI 380.05AP (1 juv), MBI 382.01DP (41 ad, 66 juv; AMS C.203419 [1 ad], MNHN [1 ad], ANSP 400821 [1 ad]), MBI 382.01AP (5 ad [2 dissected], 12 juv), MBI 383.05DP (13 ad, 18 juv), MBI 383.05AP (2 juv), MBI 384.08DP (2 ad, 2 juv), MBI 385.03DP (15 ad, 15 juv), MBI 385.03AP (2 ad [1 dissected]).

**Type locality:** Madagascar: Tulear Province: northwest of Fort Dauphin: west of village of Malio: local summit of Mount Vasiha, south of main summit, 860 m elevation: latitude 24°55'18"S, longitude 46°44'19"E: primary rain-forest.

### Description of holotype shell:

**Size and Shape.** Diameter 3.9 mm; height 4.6 mm. Height-diameter ratio 1.2. Spire angle 70 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before

body whorl constriction 0% of shell diameter. Final umbilicus 15% of shell diameter. Whorls 5.4.

**Aperture.** Aperture width parallel to parietal callus 41% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 0.94. Columellar plica absent. Apertural plane parallel to rotational axis. No apertural anal notch. No baso-columellar denticle. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 1.64. Aperture plus peristome greatest dimension angled outward from rotational axis 30 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 1.26. No peristome baso-palatal indentation. No peristome upper curl forward extension. Inner, second peristome present, projecting less than 0.01 whorl.

**Apex.** Embryonic whorls 2.1. Embryonic sculpture granular. First whorl diameter 0.55 mm. First three whorls diameter 1.56 mm.

**Sculpture on Last Tenth of Penultimate Whorl.** Transverse ribs 24; rib height 0.3% of shell diameter. No complete spiral grooves between sutures. No short spiral grooves between sutures. No spiral ridges between sutures. No spiral lines of punctae between sutures. No heringbone sculpture; no honeycomb sculpture.

**Pre-Apertural Morphology.** Body whorl constricted 0.2 whorl before aperture; constricting by 4% of whorl diameter. Body whorl sculpture not diminishing before constriction. Post-constriction body whorl swollen by 2% of constriction diameter. No secondary body whorl constriction. Transverse ribs on post-constrictional swelling numbering 8 in 0.1 whorl; rib height 0.3% of shell diameter; ribs not slanted.

**Color.** Basic color brown-orange. Apex brown-orange. One spiral color band; color white. Pre-apertural constriction red-brown. Peristome (excluding periostracum) white.

**Shell variation:** Younger, fresher shells have—in addition to the described rib sculpture—regularly, widely spaced, high-standing periostracal transverse ribs. Some adults have a slightly broader outer peristome than the holotype. During shell growth, the outer peristome forms first, so neoadults lack the inner peristome. Color varies from brown to yellow-brown. Among the 44 adults from station MBI-382, shell height ranges from 4.7 to 5.9 mm.

**Shell comparisons:** Half the size of *Boucardicus albocinctus* (Smith, 1893) and *B. antsahanori* Emberton, 1994. Larger than *B. mageti* Fischer-Piette, Blanc, Blanc & Salvat, 1993, and without its spiral striation. Younger, fresher shells are unique within the genus for their regularly, widely spaced, high-standing periostracal transverse ribs.



Explanation of Figures 2–4

Shells of Mahermana-Ilapiry-Vasiha *Boucardicus*. Figure 2. *Boucardicus esetrae* Emberton & Pearce, sp. nov., holotype. Figure 3. *Boucardicus antiquus* Emberton & Pearce, sp. nov., holotype. Figure 4. *Boucardicus delicatus* Emberton & Pearce, sp. nov., holotype. All scale bars 1 mm.



**Description of genitalia (MBI 382.01AP: 1 male, 1 female; MBI 385.03AP: 1 female):** Penis length 2.8 mm, 0.7 shell diameter. Penial papilla-ejaculatory-pore position dorsal. Penial dorsal papilla terminal, weak to no protrusion beyond tip of penis, anteriorly directed. Penis terminal swelling conspicuous, terminal-bulb width 1.3 pre-bulb width. Penial gland present. Penial-gland length 1.3 penis pre-terminal-bulb width. Penial-gland position proximal, its center 0.4 along the penis length from its base. Penial-gland attachment position dorsal. Penial-gland free lobe direction left. Base of FPSC (fertilization pouch-seminal receptacle complex): broad-based, simple. Ducted gland on base of FPSC absent. Muscular funnel within body of FPSC present. Body-and-tube shape of FPSC: upper body straight, apex-plus-tube a rounded, up-pointed, backward "S."

**Distribution:** On all three mountains, from 300 to 860 m elevation. Also apparently on Pic St. Louis (25°00'30"S, 46°57'45"E) at 500–530 m, and on Mounts Vohibololo (340–420 m) and Teloboko (640 m) near Mount Mahermana (MBI 1419, 1420, 1438–1440, 1451), all in the Vohimena Chain; in the Anosy Chain, not found north of Mount Vasiha on either Andohahela or Col Beampingaratra; no other records exist (Emberton, in press). Thus, restricted to the Vohimena and the southern Anosy chains, with a range extent of < 1,000 km<sup>2</sup>, with severely fragmented populations, and within forest habitat that is continuing to decline in extent and/or quality. Meets IUCN (1996) criteria for Endangered status.

**Etymology:** For the village of Esetra, near the type locality.

*Boucardicus antiquus* Emberton & Pearce, sp. nov.

(Figures 3, 34, 56)

*Boucardicus* n. sp. 17, Emberton, 1996:735.

*Boucardicus* sp. 2, Emberton et al., 1996:210. Emberton, 1997:1146, 1149. Emberton et al., 1999:table 2.

**Holotype:** USNM 860777 (ex MBI 387.01DH, adult shell).

**Paratypes:** MBI 373.13DP (1 ad, 4 juv), MBI 373.13AP (1 ad), MBI 375.05DP (1 ad), MBI 376.05DP (1 juv), MBI 376.05AP (2 ad), MBI 377.06DP (1 ad, 1 juv), MBI 378.08DP (1 ad, 1 juv), MBI 379.08DP (6 ad, 4 juv), MBI 379.08AP (2 ad, 2 juv), MBI 380.06DP (1 ad), MBI 385.04DP (1 juv), MBI 386.06DH (4 ad, 3 juv), MBI 386.06AP (2 ad, 2 juv), MBI 387.01DP (10 ad, 16 juv; AMS C.203420 [1 ad]; MNHN [1 ad]; ANSP 400822 [1 ad]), MBI 387.01AP (4 ad [2 dissected], 2 juv), MBI 390.01DP (1 ad, 1 juv).

**Type locality:** Madagascar: Tulear Province: northwest of Fort Dauphin: west of village of Malio: eastsoutheast-facing slope of Mount Vasiha, 200 m elevation: latitude 24°56'13"S, longitude 46°45'13"E: primary rainforest.

#### Description of holotype shell:

**Size and Shape.** Diameter 3.2 mm; height 5.5 mm. Height-diameter ratio 1.7. Spire angle 65 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 0% of shell diameter. Final umbilicus 5% of shell diameter. Whorls 6.5.

**Aperture.** Aperture width parallel to parietal callus 39% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 1.00. Columellar plica present. Apertural plane inclined downward; 5 degrees from rotational axis. Apertural anal notch 26% of apertural width. No baso-columellar denticle. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 1.74. Aperture plus peristome greatest dimension angled outward from rotational axis 35 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 1.28. No peristome baso-palatal indentation. No peristome upper curl forward extension. Inner, second peristome present, projecting more than 0.01 whorl.

**Apex.** Embryonic whorls 2.2. Embryonic sculpture smooth then transverse ribs. First whorl diameter 0.54 mm. First three whorls diameter 1.06 mm.

**Sculpture on Last Tenth of Penultimate Whorl.** Transverse ribs 11; rib height 0.9% of shell diameter. No complete spiral grooves between sutures. No short spiral grooves between sutures. No spiral ridges between sutures. No spiral lines of punctae between sutures. No herringbone sculpture; no honeycomb sculpture.

**Pre-Apertural Morphology.** Body whorl constricted 0.6 whorl before aperture; constricting by less than 0.5% of whorl diameter. Body whorl sculpture diminishes 90% before constriction. Post-constriction body whorl swollen by 26% of constriction diameter. No secondary body whorl constriction. Transverse ribs on post-constrictional swelling numbering 11 in 0.1 whorl; rib height 0.9% of shell diameter; ribs not slanted.

**Color.** Basic color white. Apex white. No spiral color bands. Pre-apertural constriction white. Peristome (excluding periostracum) white.

**Shell variation:** As in *Boucardicus esetrae* sp. nov., the outer peristome forms first, so some neoadults lack the inner peristome. No other conspicuous variation in shape or size.

**Shell comparisons:** Shorter than *Boucardicus villae* (Fischer-Piette, Blanc, Blanc & Salvat, 1993) and with a narrower apertural anal notch and a much greater preapertural swelling of the body-whorl. With a smaller aperture than *B. fauri* (Fischer-Piette, Blanc, Blanc & Salvat, 1993), greater preapertural swelling, lesser umbilical major spiral ridge, and without any forward curl of the upper peristome.



**Description of reproductive characters (MBI 387.01AP: 1 male, 1 female):** Penis length 2.2 mm, 0.7 shell diameter. Penial papilla-ejaculatory-pore position dorsal. Penial dorsal papilla subterminal. Penis terminal swelling conspicuous, terminal-bulb width 1.4 pre-bulb width. Penial gland present. Penial-gland length 0.6 penis pre-terminal-bulb width. Penial-gland position proximal, its center 0.4 along the penis length from its base. Penial-gland attachment position dorsal. Penial-gland free lobe direction undetectable. Base of FPSC (fertilization pouch-seminal receptacle complex) broad-based, simple. Ducted gland on base of FPSC absent. Muscular funnel within body of FPSC absent. Body-and-tube shape of FPSC: upper body straight, apex-plus-tube a rounded, up-pointed, backward "S."

**Distribution:** On all three mountains, 100–600 m elevation and below. Also apparently on Pic St. Louis (25°00'30"S, 46°57'45"E) at 380–530 m, and on Mounts Vohibololo (110–310 m), Teloboko (530–640 m), and Esetra (summit), near Mount Mahermana (MBI 1419, 1424, 1436, 1441–1443, 1451–1453, 1493), all in the Vohimena Chain; in the Anosy Chain, found on Andohahela (430–600 m: MBI 799, 1659) but not Col Beampingaratra; outside the Vohimena-Anosy region, *Boucardicus antiquus* sp. nov. ranges northward, having been found east of Midongy at 80 m (23°23'20"S, 47°20'02"E), east of Andringitra Reserve at 1400 m (22°04'S, 46°54'E), and at Kianjavato at 200–430 m (21°22'20"S, 47°52'05"E) (MBI 1375, 1402, 1380, 1387), but not north of Kianjavato (Emberton, in press). Thus, this species is apparently restricted to the southern third of Madagascar's eastern rainforest, with a range extent of well under 20,000 km<sup>2</sup>, with severely fragmented populations, and within forest habitat that is continuing to decline in extent and/or quality. Meets IUCN (1996) criteria for Vulnerable status.

**Etymology:** Named for the antique (Latin *antiquus*) appearance of the shell.

*Boucardicus delicatus* Emberton & Pearce, sp. nov.

(Figures 4, 35, 57)

*Boucardicus* sp. 3, Emberton et al., 1996:210. Emberton, 1997:1147. Emberton et al., 1999:table 2.

**Holotype:** USNM 860778 (ex MBI 385.01DH, adult shell).

**Paratypes:** MBI 379.09DP (1 ad), MBI 379.09AP (2 ad, 1 juv), MBI 381.07DP (1 ad, 1 juv), MBI 382.08DP (1 ad), MBI 384.09DP (1 ad), MBI 385.01DP (1 ad, 2 juv; AMS C.203421 [1 ad]; MNHN [1 ad]), MBI 385.01AP (3 ad [2 dissected], 2 juv), MBI 386.07DP (2 ad).

**Type locality:** Madagascar: Tulear Province: northwest of Fort Dauphin: west of village of Malio: eastsoutheast-facing valley on Mount Vasiha, 400 m elevation: latitude 24°55'25"S, longitude 46°44'45"E: primary rainforest.

#### Description of holotype shell:

**Size and Shape.** Diameter 1.1 mm; height 1.8 mm. Height-diameter ratio 1.7. Spire angle 65 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 0% of shell diameter. Final umbilicus 0% of shell diameter. Whorls 4.6.

**Aperture.** Aperture width parallel to parietal callus 37% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 1.09. Columellar plica absent. Apertural plane inclined downward; 5 degrees from rotational axis. No apertural anal notch. Baso-columellar denticle present; size 25% of apertural width; depth 0.00 whorl. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 1.81. Aperture plus peristome greatest dimension angled outward from rotational axis 50 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 1.14. Peristome baso-palatal indentation 50% of basal peristome width. No peristome upper curl forward extension. Inner, second peristome absent.

**Apex.** Embryonic whorls 2.0. Embryonic sculpture smooth. First whorl diameter 0.30 mm. First three whorls diameter 0.76 mm.

**Sculpture on Last Tenth of Penultimate Whorl.** No transverse ribs. No complete spiral grooves between sutures. No short spiral grooves between sutures. No spiral ridges between sutures. No spiral lines of punctae between sutures. Fourteen herringbones; no honeycomb sculpture.

**Pre-Apertural Morphology.** Body whorl constricted 0.3 whorl before aperture; constricting by 4% of whorl diameter. Body whorl sculpture not diminishing before constriction. Post-constriction body whorl swollen by 21% of constriction diameter. No secondary body whorl constriction. Transverse ribs on post-constrictional swelling numbering 10 in 0.1 whorl; rib height less than 0.05% of shell diameter; ribs not slanted.

**Color.** Basic color white-brown. Apex brown-white. No spiral color bands. Pre-apertural constriction white-brown. Peristome (excluding periostracum) white.

**Shell variation:** No conspicuous variation in size or shape.

**Shell comparisons:** Unique in its combination of minute size, high-spined shape, and herringbone sculpture. Most similar to *Boucardicus randalanai* sp. nov., from which it differs in its smaller, more ovate aperture.

**Description of reproductive characters (MBI 387.01AP: 1 male, 1 female):** Penis length 0.9 mm, 0.8 shell diameter. Penial papilla-ejaculatory-pore position central. Penis terminal swelling slight, terminal-bulb width 1.1 pre-bulb width. Penial gland absent. Base of

FPSC (fertilization pouch-seminal receptacle complex) undetectable. Ducted gland on base of FPSC absent. Body-and-tube shape of FPSC: upper body straight, apex-plus-tube a rounded, up-pointed, backward "S."

**Local distribution:** On Mounts Ilapiry and Vasiha, 200–400 m elevation. Not found in the northern Vohimena chain; also found on Andohahela, 430–1600 m (MBI 771, 772, 780, 781, 789, 791, 799), but not at Col Beampingaratra (Emberton, in press). Thus, apparently restricted to the southern Anosy and Vohimena chains, with a range extent < 1,000 km<sup>2</sup>, with severely fragmented populations, and within forest habitat that is continuing to decline in extent and/or quality. Meets IUCN (1996) criteria for Endangered status.

**Etymology:** The tiny shell is very thin and fragile (Latin *delicatus*).

*Boucardicus curvifolius* Emberton & Pearce,  
sp. nov.

(Figures 5, 36, 58)

*Boucardicus* n. sp. 21, Emberton, 1996:735.

*Boucardicus* sp. 4, Emberton et al., 1996:210. Emberton, 1997:1146, 1149. Emberton et al., 1999:table 2.

**Holotype:** USNM 860779 (ex MBI 381.01DH, adult shell).

**Paratypes:** MBI 373.22AP (2 ad), MBI 377.21AP (1 ad), MBI 379.32AP (3 ad), MBI 380.07DP (1 ad), MBI 380.07AP (7 ad [1 dissected], 1 juv), MBI 381.01DP (3 ad; AMS C.203422 [1 ad]; MNHN [1 ad]; ANSP 400823 [1 ad]), MBI 381.01AP (2 ad [2 dissected], 3 juv).

**Type locality:** Madagascar: Tulear Province: north of Fort Dauphin: west of village of Mahialambo: east-south-east-facing slope of Mount Ilapiry, 200 m elevation: latitude 24°51'39"S, longitude 47°00'46"E: primary rainforest.

#### Description of holotype shell:

**Size and Shape.** Diameter 3.5 mm; height 3.2 mm. Height-diameter ratio 0.9. Spire angle 70 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 0% of shell diameter. Final umbilicus 16% of shell diameter. Whorls 4.2.

**Aperture.** Aperture width parallel to parietal callus 31% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 0.88. Columellar plica absent. Apertural plane inclined upward; 10 degrees from rotational axis. No apertural anal notch. No baso-columellar denticle. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 2.18. Aperture plus peristome greatest dimension angled outward from rotational axis 15 degrees. Ratio of aperture plus peristome

greatest width to aperture plus peristome greatest height as measured perpendicular to width line 1.51. Peristome baso-palatal indentation 42% of basal peristome width. Peristome upper curl extends forward 82% of upper peristome width. Inner, second peristome present, projecting less than 0.01 whorl.

**Apex.** Embryonic whorls 2.0. Embryonic sculpture smooth with faint traces of growth lines. First whorl diameter 0.74 mm. First three whorls diameter 1.98 mm.

**Sculpture on Last Tenth of Penultimate Whorl.** No transverse ribs. No complete spiral grooves between sutures. No short spiral grooves between sutures. No spiral ridges between sutures. No spiral lines of punctae between sutures. No herringbone sculpture; no honeycomb sculpture.

**Pre-Apertural Morphology.** Body whorl constricted 0.4 whorl before aperture; constricting by 11% of whorl diameter. Lack of body whorl sculpture continues into constriction. Post-constriction body whorl swollen by 11% of constriction diameter. Secondary body whorl constriction present; swelling after secondary constriction enlarged by 34% of diameter of first constriction. Transverse ribs on post-constrictional swelling numbering 14 in 0.1 whorl; rib height 1.4% of shell diameter; ribs slanting backward; 60 degrees.

**Color.** Basic color brown. Apex red-brown. Two spiral color bands; color yellow-white. Pre-apertural constriction yellow-white. Peristome (excluding periostracum) yellow-white.

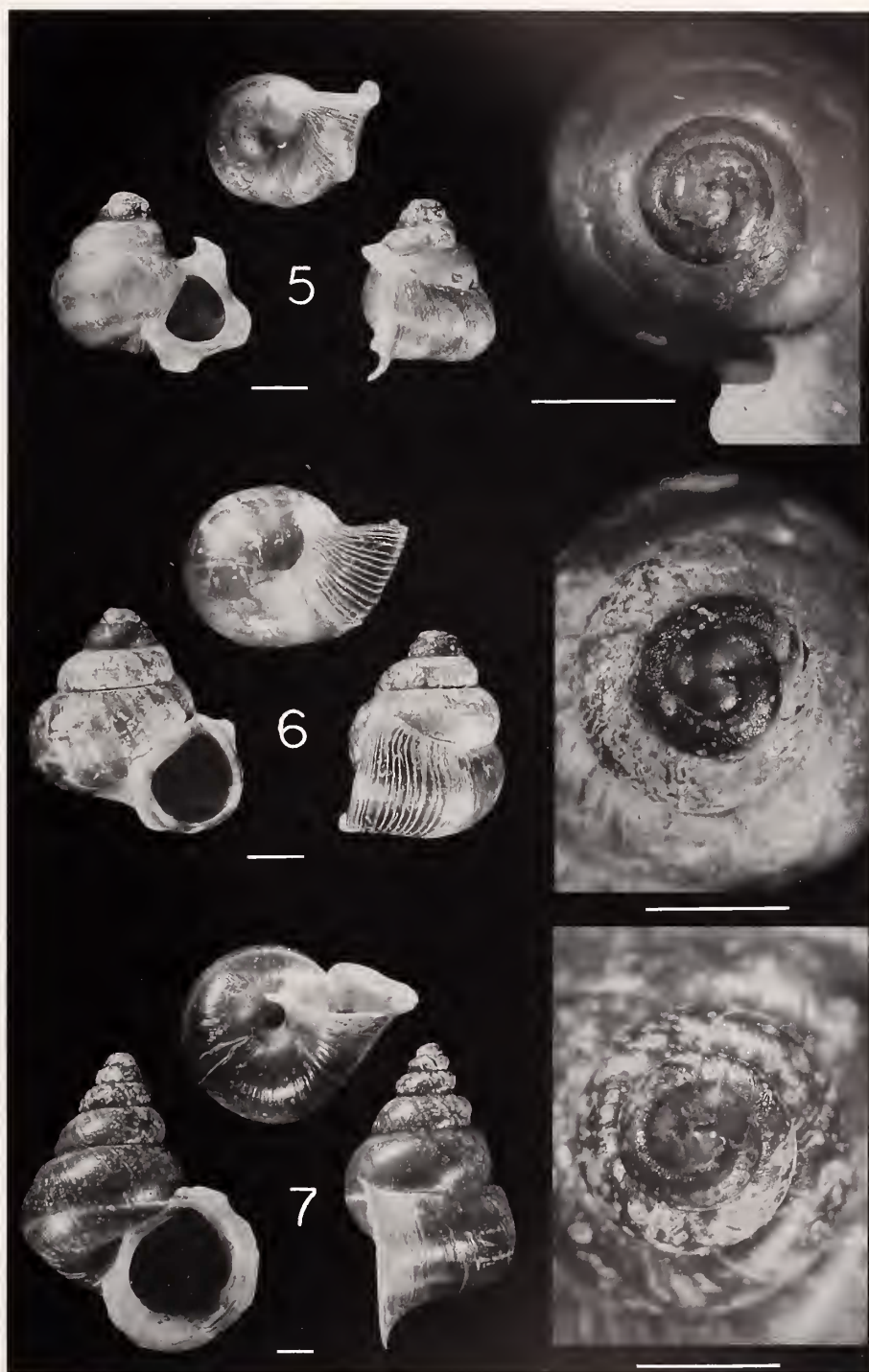
**Shell variation:** No conspicuous variation in size or shape.

**Shell comparisons:** Unique in its flamboyantly tri-lobed apertural peristome.

**Description of reproductive characters (MBI 380.07AP: 1 male; MBI 381.01AP: 1 male, 1 female):** Penis length 2.5 mm, 0.7 shell diameter. Penial papilla-ejaculatory-pore position dorsal. Penial dorsal papilla terminal, weak to no protrusion beyond tip of penis, anteriorly directed. Penis terminal swelling slight, terminal-bulb width 1.2 pre-bulb width. Penial gland present. Penial-gland length 2.0 penis pre-terminal-bulb width. Penial-gland position distal, its center 0.8 along the penis length from its base. Penial-gland attachment position ventral. Penial-gland free lobe direction left. Base of FPSC (fertilization pouch-seminal receptacle complex) broad-based, simple. Ducted gland on base of FPSC absent. Muscular funnel within body of FPSC present. Body-and-tube shape of FPSC: upper mid-body folded left, apex-plus-tube a squashed, backward "S."

**Distribution:** Known only from the Vohimena chain (Mt. Mahermana and Mt. Ilapiry), from 200 to 540 m elevation. One other locality (Emberton, in press) is also in the Vohimena chain: Pic St. Jacques (24°58'00"S, 46°57'25"E), 520 m (MBI 1431). Thus, restricted to the





## Explanation of Figures 5–7

Shells of Mahermana-Ilapiry-Vasiha *Boucardicus*. Figure 5. *Boucardicus curvifolius* Emberton & Pearce, sp. nov., holotype. Figure 6. *Boucardicus victorhernandezii* Emberton, 1998 b, holotype. Figure 7. *Boucardicus albocinctus* (Smith, 1893), representative from Mount Mahermana. All scale bars 1 mm.



Vohimena chain, with a range extent of < 500 km<sup>2</sup>, with severely fragmented populations, and within forest habitat that is continuing to decline in extent and/or quality. Meets IUCN (1996) criteria for Endangered status.

**Etymology:** From the peristome resembling a curled (Latin *curvi-*) leaf (*L. folius*).

*Boucardicus victorhernandezii* Emberton, 1998

(Figures 6, 59)

*Boucardicus* sp. 5, Emberton et al., 1996:210. Emberton, 1997:1147. Emberton et al., 1999:table 2.

**Description of holotype shell (from Emberton, 1998):**

**"Size and Shape.** Diameter 3.7 mm; height 3.8 mm. Height-diameter ratio 1.0. Spire angle 80 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 0% of shell diameter. Final umbilicus 29% of shell diameter. Whorls 4.5."

**"Aperture.** Aperture width parallel to parietal callus 38% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 0.87. Columellar plica absent. Apertural plane inclined upward; 5 degrees from rotational axis. No apertural anal notch. No baso-columellar denticle. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 1.54. Aperture plus peristome greatest dimension angled outward from rotational axis 35 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 1.32. Peristome baso-palatal indentation 23% of basal peristome width. Peristome upper curl extends forward 17% of upper peristome width. Inner, second peristome present, projecting less than 0.01 whorl."

**"Apex.** Embryonic whorls 2.0. Embryonic sculpture granular with faint traces of growth lines. First whorl diameter 0.75 mm. First three whorls diameter 2.10 mm."

**"Sculpture on Last Tenth of Penultimate Whorl.** Transverse ribs 22; rib height less than 0.05% of shell diameter. No complete spiral grooves between sutures. No short spiral grooves between sutures. No spiral ridges between sutures. No spiral lines of punctae between sutures. No herringbone sculpture; no honeycomb sculpture."

**"Pre-Apertural Morphology.** Body whorl constricted 0.3 whorl before aperture; constricting by 11% of whorl diameter. Body whorl sculpture not diminishing before constriction. Post-constriction body whorl swollen by 10% of constriction diameter. No secondary body whorl constriction. Transverse ribs on post-constrictional swelling numbering 10 in 0.1 whorl; rib height 1.1% of shell diameter; ribs slanting forward; 80 degrees."

**"Color.** Basic color brown-red. Apex dark brown-red. One spiral color band; color white. Pre-apertural constrict-

tion white. Peristome (excluding periostracum) white and red-brown."

**Description of reproductive characters (MBI 373.23AP: 1 female):** Penial morphology unknown. Base of FPSC (fertilization pouch-seminal receptacle complex) broad-based, simple. Ducted gland on base of FPSC absent. Muscular funnel within body of FPSC present. Body-and-tube shape of FPSC: upper mid-body folded left, apex-plus-tube a squashed, backward "S."

**Distribution:** Restricted to the Vohimena Mountain Chain; known from only four of eight sampled peaks within the chain; proposed for Endangered status (Emberton, 1998).

*Boucardicus albocinctus* (E. A. Smith, 1893)

(Figures 7, 28, 32, 37, 38, 49–51, 53, 61)

*Boucardicus albocinctus* (Smith, 1893). Emberton, 1996: 735.

*Boucardicus* sp. 6, Emberton et al., 1996:210. Emberton, 1997:1146, 1149. Emberton et al., 1999:table 2.

**Representative:** MBI 373.01DR (ad).

**Other specimens:** MBI 373.01D (0; AMS C.203424 [1 ad]), MBI 373.01A (3 Zad [2 dissected]), MBI 374.06D (1 ad, 2 juv), MBI 374.06A (1 ad), MBI 375.06D (1 juv), MBI 375.06A (1 juv), MBI 377.08D (2 ad), MBI 390.05A (2 ad).

**Description of representative shell:**

**Size and Shape.** Diameter 6.5 mm; height 8.2 mm. Height-diameter ratio 1.3. Spire angle 50 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 2% of shell diameter. Final umbilicus 9% of shell diameter. Whorls 5.9.

**Aperture.** Aperture width parallel to parietal callus 45% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 0.97. Columellar plica absent. Apertural plane parallel to rotational axis. No apertural anal notch. No baso-columellar denticle. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 1.68. Aperture plus peristome greatest dimension angled outward from rotational axis 40 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 1.24. No peristome baso-palatal indentation. Peristome upper curl extends forward 28% of upper peristome width. Inner, second peristome absent.

**Apex.** Embryonic whorls 2.0. Embryonic sculpture granular with faint traces of growth lines. First whorl diameter 0.78 mm. First three whorls diameter 1.88 mm.

**Sculpture on Last Tenth of Penultimate Whorl.** Transverse ribs 18; rib height 0.2% of shell diameter. Sixty complete spiral grooves between sutures; complete spiral

grooves slightly wavy. No short spiral grooves between sutures. No spiral ridges between sutures. No spiral lines of punctae between sutures. No herringbone sculpture; no honeycomb sculpture.

**Pre-Apertural Morphology.** Body whorl constricted 0.1 whorl before aperture; constricting by 4% of whorl diameter. Body whorl sculpture not diminishing before constriction. Post-constriction body whorl swollen by 0% of constriction diameter. No secondary body whorl constriction. Transverse ribs on post-constrictional swelling numbering 12 in 0.1 whorl; rib height 1.2% of shell diameter; ribs slanting forward; 90 degrees.

**Color.** Basic color brown-red. Apex dark brown-red. One spiral color band; color white. Pre-apertural constriction brown-red. Peristome (excluding periostracum) white and red-brown.

**Local shell variation:** The one adult from station MBI 374 has a more oval, less circular aperture than the representative.

**Description of reproductive characters (MBI 373.01A: 1 male, 1 female [mating pair]):** Penis length 5.6 mm, 0.9 shell diameter. Penial papilla-ejaculatory-pore position dorsal. Penial dorsal papilla terminal, weak to no protrusion beyond tip of penis, anteriorly directed. Penis terminal swelling conspicuous, terminal-bulb width 1.6 pre-bulb width. Penial gland present. Penial-gland length 1.2 penis pre-terminal-bulb width. Penial-gland position proximal, its center 0.3 along the penis length from its base. Penial-gland attachment position dorsal. Penial-gland free lobe direction right. Base of FPSC (fertilization pouch-seminal receptacle complex) narrow-based, with multiple apical lobes. Ducted gland on base of FPSC absent. Muscular funnel within body of FPSC absent. Body-and-tube shape of FPSC: upper mid-body folded left, apex-plus-tube a squashed, backward "S."

**Distribution:** On the two eastern, Vohimena-Chain mountains (Mts. Mahemana and Ilapiry) from 200 to 540 m elevation. Apparently a very wide-ranging species within Madagascar's eastern rainforest. Fischer-Piette et al. (1993) gave records from Périnet and Anosibe. Emberton (in press) reported it from many sites, including Andohahela and Beampingaratra in the Anosy chain, the northernmost of which is Betampona Reserve, northwest of Tamatave (17°55'05"S, 49°12'00"E), but no farther north. Thus, this species is apparently restricted to the southern two-thirds of Madagascar's eastern rainforest, with a range < 20,000 km<sup>2</sup>, with severely fragmented populations, and within forest habitat that is continuing to decline in extent and/or quality. Meets IUCN (1996) criteria for Vulnerable status.

### *Boucardicus divei*

Fischer-Piette, Blanc, Blanc & Salvat, 1993

(Figures 8, 30, 39, 60)

*Boucardicus* sp. 7, Emberton et al., 1996:210. Emberton, 1997:1146, 1149. Emberton et al., 1999:table 2.

**Representative:** MBI 376.01DR (ad).

**Other specimens:** MBI 373.24A (1 ad), MBI 374.07D (1 ad), MBI 375.07D (1 ad), MBI 375.07A (1 ad), MBI 376.01D (1 ad, 2 juv), MBI 376.01A (1 ad [dissected]), MBI 377.09D (4 ad), MBI 377.09A (2 ad), MBI 378.09D (1 ad), MBI 378.09A (1 ad, 3 juv), MBI 379.10D (6 ad), MBI 379.10A (3 ad, 1 juv), MBI 380.24A (1 ad [dissected]), MBI 382.26A (1 ad), MBI 388.02D (16 ad, 6 juv; AMS C.203425 [1 ad]; MNHN [1 ad]; ANSP 400824 [1 ad]), MBI 388.02A (1 ad).

### **Description of representative shell:**

**Size and Shape.** Diameter 5.0 mm; height 5.5 mm. Height-diameter ratio 1.1. Spire angle 75 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 2% of shell diameter. Final umbilicus 13% of shell diameter. Whorls 4.8.

**Aperture.** Aperture width parallel to parietal callus 41% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 0.97. Columellar plica absent. Apertural plane inclined downward; 5 degrees from rotational axis. No apertural anal notch. No baso-columellar denticle. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 1.48. Aperture plus peristome greatest dimension angled outward from rotational axis 40 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 1.09. No peristome baso-palatal indentation. No peristome upper curl forward extension. Inner, second peristome absent.

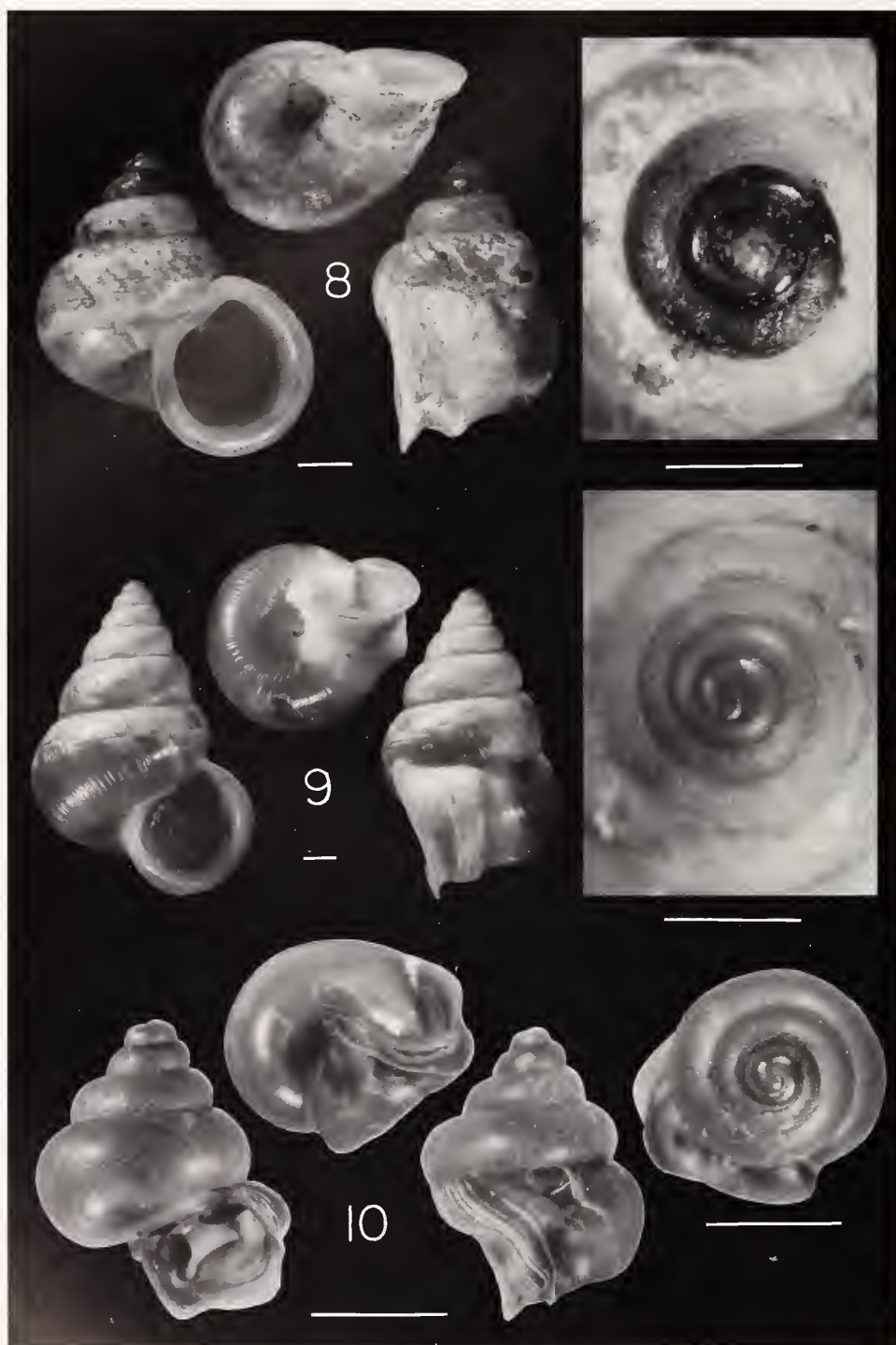
**Apex.** Embryonic whorls 2.1. Embryonic sculpture smooth then slightly granular. First whorl diameter 0.73 mm. First three whorls diameter 2.10 mm.

**Sculpture on Last Tenth of Penultimate Whorl.** Transverse ribs 9; rib height less than 0.05% of shell diameter. No complete spiral grooves between sutures. No short spiral grooves between sutures. Seven spiral ridges between sutures; spiral ridges 1.00 mm high; spiral ridges moderately wavy. No spiral lines of punctae between sutures. No herringbone sculpture; no honeycomb sculpture.

**Pre-Apertural Morphology.** Body whorl constricted 0.1 whorl before aperture; constricting by less than 0.5% of whorl diameter. Body whorl sculpture not diminishing before constriction. Post-constriction body whorl swollen by 0% of constriction diameter. Secondary body whorl constriction present; swelling after secondary constriction enlarged by 0% of diameter of first constriction. Transverse ribs on post-constrictional swelling numbering 17 in 0.1 whorl; rib height 0.4% of shell diameter; ribs slanting forward; 10 degrees.

**Color.** Basic color light yellow-brown. Apex dark red-brown. One spiral color band; color white. Pre-apertural constriction white. Peristome (excluding periostracum) white.





#### Explanation of Figures 8–10

Shells of Mahermana-Ilapiry-Vasiha *Boucardicus*. Figure 8, *Boucardicus divei* Fischer-Piette, Blanc, Blanc & Salvat, 1993, representative from Mount Mahermana. Figure 9, *Boucardicus culminans* Fischer-Piette, Blanc, Blanc & Salvat, 1993, representative from Mount Mahermana. Figure 10, *Boucardicus tridentatus* Emberton & Pearce, sp. nov., holotype. All scale bars 1 mm.



**Shell variation:** Among the six adults from station MBI-379, shell height ranges from 4.4 to 5.1 mm. This is greater than the height variation among the 19 adults from MBI-388.

**Description of reproductive characters (MBI 376.01A: 1 female; MBI 380.24A: 1 male):** Penis length 3.0 mm, 0.6 shell diameter. Penial papilla-ejaculatory-pore position dorsal. Penial dorsal papilla terminal, little protrusion, ventrally directed. Penis terminal swelling undetectable, terminal-bulb width 1.0 pre-bulb width. Penial gland present. Penial-gland length 1.4 penis pre-terminal-bulb width. Penial-gland position proximal, its center 0.3 along the penis length from its base. Penial-gland dorso-ventral attachment position dorsal. Penial-gland free lobe direction undetectable. Base of FPSC (fertilization pouch-seminal receptacle complex) broad-based, then with narrow, subapical extension. Ducted gland on base of FPSC present. Muscular funnel within body of FPSC absent. Body-and-tube shape of FPSC: upper body straight, apex-plus-tube a rounded, up-pointed, backward "S."

**Local distribution:** On all three mountains, from 100 to 860 m elevation. Originally described from the Anosy chain (north of Mt. Vasiha), at about 1000 m elevation (Fischer-Piette et al., 1993). Also found at 800 m on Andohahela, Anosy chain (Emberton, in press: MBI 800), but nowhere else. Thus, apparently restricted to the Anosy and Vohimena chains, with a range extent well under 5000 km<sup>2</sup>, with severely fragmented populations, and within forest habitat that is continuing to decline in extent and/or quality. Meets IUCN (1996) criteria for Endangered status.

### *Boucardicus culminans*

Fischer-Piette, Blanc, Blanc & Salvat, 1993

(Figures 9, 40, 52, 54, 62)

*Boucardicus culminans* Fischer-Piette et al., 1993, Emberton, 1996:735.

*Boucardicus* sp. 8, Emberton et al., 1996:210. Emberton, 1997:1147. Emberton et al., in press:table 2.

**Representative:** MBI 376.02DR (ad).

**Other specimens:** MBI 374.08D (1 juv), MBI 376.02D (2 juv; AMS C. 203426 [1 ad fragment]) MBI 390.06A (2 ad [2 dissected]).

### **Description of representative shell:**

**Size and Shape.** Diameter 6.5 mm; height 9.1 mm. Height-diameter ratio 1.4. Spire angle 55 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 2% of shell diameter. Final umbilicus 12% of shell diameter. Whorls 7.0.

**Aperture.** Aperture width parallel to parietal callus 34% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 1.09. Colu-

mellar plica absent. Apertural plane inclined downward; 15 degrees from rotational axis. No apertural anal notch. No baso-columellar denticle. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 1.45. Aperture plus peristome greatest dimension angled outward from rotational axis 35 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 1.26. No peristome baso-palatal indentation. No peristome upper curl forward extension. Inner, second peristome absent.

**Apex.** Embryonic whorls 1.9. Embryonic sculpture smooth then slightly granular. First whorl diameter 0.60 mm. First three whorls diameter 1.60 mm.

**Sculpture on Last Tenth of Penultimate Whorl.** Transverse ribs 20; rib height 0.5% of shell diameter. No complete spiral grooves between sutures. No short spiral grooves between sutures. No spiral ridges between sutures. No spiral lines of punctae between sutures. No her-ringbone sculpture; no honeycomb sculpture.

**Pre-Apertural Morphology.** Body whorl constricted 0.1 whorl before aperture; constricting by 1% of whorl diameter. Body whorl sculpture diminishes 80% before constriction. Post-constriction body whorl swollen by 18% of constriction diameter. No secondary body whorl constriction. Transverse ribs on post-constrictional swelling numbering 16 in 0.1 whorl; rib height 0.2% of shell diameter; ribs not slanted.

**Color.** Basic color light yellow-brown. Apex light yellow-brown. No spiral color bands. Pre-apertural constriction yellow-white. Peristome (excluding periostracum) yellow-white.

### **Description of reproductive characters (MBI 390.06A:**

**1 male, 1 female):** Penis length 9.8 mm, 1.5 shell diameter. Penial papilla-ejaculatory-pore position ventral. Penis terminal swelling conspicuous, terminal-bulb width 1.3 pre-bulb width. Penial gland present. Penial-gland length 2.3 penis pre-terminal-bulb width. Penial-gland position central, its center 0.6 along the penis length from its base. Penial-gland attachment position ventral. Penial-gland free lobe direction left. Base of FPSC (fertilization pouch-seminal receptacle complex) broad-based, simple. Ducted gland on base of FPSC absent. Muscular funnel within body of FPSC present. Body-and-tube shape of FPSC: upper body straight, apex-plus-tube a rounded, up-pointed, backward "S."

**Distribution:** In our samples, it occurred only on Mt. Mahermana from 100 to 300 m elevation. Also reported (Emberton, in press) from Mounts Mahermana and Varabe (Vohimena Chain); from Col Beampingaratra (Anosy Chain); and 40 km east of Midongy (MBI 1445, 1448, 1499, 1458, 1372). Fischer-Piette et al. (1993) described *Boucardicus culminans* from four shells from an Anosy-Chain summit at 1900 m and from a juvenile shell col-

lected in 1950 by Millot at "Ivohibe," a locality which Fischer-Piette et al. (1993) considered to be near Andringitra. Although their description gives the range of *B. culminans* as "Madagascar Sud-Est," their range map shows a third, uncited locality in the far northeast at Marojejy. We have collected extensively in the Andringitra area and on Marojejy and environs without finding *B. culminans* (Emberton, in press). We conclude that the Marojejy locality is spurious and that the "Ivohibe" juvenile shell was either misidentified or was actually from Varabe, Vohimena Chain, which lies very near the road north of Fort Dauphin (so might well have been visited by Millot) and is referred to by locals as "Ivohibe." Thus it seems likely that this species ranges from the northern Vohimena and Anosy chains north to the Midongy area. This would give it a range of well under 5000 km<sup>2</sup>, with severely fragmented populations in forest habitat that is continuing to decline in extent and/or quality of habitat. *B. culminans* therefore meets IUCN (1996) criteria for Endangered status.

*Boucardicus tridentatus* Emberton & Pearce,  
sp. nov.

(Figures 10, 11, 41, 63)

*Boucardicus* sp. 9, Emberton et al., 1996:209, 210. Emberton, 1997:1146, 1149. Emberton et al., in press:table 2.

**Holotype:** USNM 860780 (ex MBI 385.02DH, adult shell).

**Paratypes:** MBI 373.14DP (1 juv), MBI 373.14AP (2 juv), MBI 374.09DP (1 juv), MBI 375.08DP (1 ad, 1 juv), MBI 375.08AP (2 ad), MBI 376.06DP (1 ad, 1 juv), MBI 376.06AP (2 ad), MBI 378.19AP (1 juv), MBI 379.11DP (2 ad), MBI 379.11AP (2 ad, 1 juv), MBI 380.09DP (1 ad), MBI 382.27AP (2 ad, 1 juv), MBI 383.06DP (1 ad), MBI 383.06AP (4 ad), MBI 384.10DP (1 ad), MBI 384.10AP (1 ad), MBI 385.02DP (10 ad; AMS C.203427 [1 ad]; MNHN [1 ad]; ANSP 400825 [1 ad]), MBI 385.02AP (11 ad [2 dissected], 4 juv), MBI 386.14AP (1 juv), MBI 387.04DP (6 ad, 2 juv), MBI 387.04AP (4 ad, 1 juv).

**Type locality:** Madagascar: Tulear Province: northwest of Fort Dauphin: west of village of Malio: eastsoutheast-facing valley on Mount Vasiha, 400 m elevation: latitude 24°55'25"S, longitude 46°44'45"E: primary rainforest.

**Description of holotype shell:**

*Size and Shape.* Diameter 1.8 mm; height 2.2 mm. Height-diameter ratio 1.2. Spire angle 70 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 3% of shell diameter. Final umbilicus 15% of shell diameter. Whorls 4.5.

*Aperture.* Aperture width parallel to parietal callus 42% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 0.67. Colu-

mellar plica absent. Apertural plane inclined downward; 35 degrees from rotational axis. No apertural anal notch. Baso-columellar denticle present; size 32% of apertural width; depth 0.20 whorl. Basal denticle present; size 20% of apertural width; depth 0.05 whorl. Upper palatal denticle present; size 33% of apertural width; depth 0.20 whorl. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 1.42. Aperture plus peristome greatest dimension angled outward from rotational axis 55 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 1.06. Peristome basopalatal indentation 27% of basal peristome width. No peristome upper curl forward extension. Inner, second peristome absent.

*Apex.* Embryonic whorls 1.8. Embryonic sculpture smooth then granular. First whorl diameter 0.37 mm. First three whorls diameter 1.05 mm.

*Sculpture on Last Tenth of Penultimate Whorl.* No transverse ribs. No complete spiral grooves between sutures. No short spiral grooves between sutures. No spiral ridges between sutures. No spiral lines of punctae between sutures. Ten herringbones; no honeycomb sculpture.

*Pre-Apertural Morphology.* Body whorl constricted 0.4 whorl before aperture; constricting by 8% of whorl diameter. Body whorl sculpture diminishes 50% before constriction. Post-constriction body whorl swollen by 36% of constriction diameter. Secondary body whorl constriction present; swelling after secondary constriction enlarged by 91% of diameter of first constriction. Transverse ribs on post-constrictional swelling numbering 14 in 0.1 whorl; rib height 1.7% of shell diameter; ribs slanting forward; 90 degrees.

*Color.* Basic color brown. Apex brown. No spiral color bands. Pre-apertural constriction brown. Peristome (excluding periostracum) brown.

**Shell variation:** No conspicuous variation in size or shape.

**Shell comparisons:** Most similar to *Boucardicus andringitrae* Fischer-Piette, Blanc, Blanc & Salvat, 1993, but smaller, taller, and with very different apertural and preapertural morphology.

**Description of reproductive characters (MBI 385.02AP: 1 male, 1 female):**

Penis length 1.3 mm, 0.7 shell diameter. Penial papilla-ejaculatory-pore position dorsal. Penial dorsal papilla terminal, strong protrusion, anteriorly directed. Penis terminal swelling slight, terminal-bulb width 1.1 pre-bulb width. Penial gland absent. Base of FPSC (fertilization pouch-seminal receptacle complex) broad-based, with fingerlike basal appendage. Ducted gland on base of FPSC absent. Body-and-tube



shape of FPSC: upper body bent right and downward, apex-plus-tube an up-pointed "U."

**Distribution:** On all three mountains, through the full range of elevations (100–860 m). Also found on three other peaks in the Vohimena Chain (St. Louis, Vohibololo, and Esetra); in two patches of coastal forest (Ste. Luce and 2.1 km south of Manambato) east of the northern Vohimena Chain; east of Midongy; and in Manombo Reserve (23°01'S, 47°44'E); but nowhere else. Thus *Boucardicus tridentatus*'s range seems limited to the leeward rainforests from Manombo south to Pic St. Louis, and to only the southernmost Anosy Chain. This is well under 5000 km<sup>2</sup> of declining and degrading forest, within which *B. tridentatus* exists in isolated subpopulations separated by cleared land. Thus this is an Endangered species under IUCN (1996) criteria.

**Comments:** During shell ontogeny, the columellar denticle starts formation low, simultaneous with the formation of the palatal denticle, and before formation of the basal denticle (Figure 11).

**Etymology:** For the three (*L. tri*-) teeth (*L. dentatus*) in the aperture.

*Boucardicus rakotoarisoni* Emberton & Pearce,  
sp. nov.

(Figures 12, 27, 42, 43, 64)

*Boucardicus* n. sp. 27, in part, Emberton, 1996:735.

*Boucardicus* sp. 10, Emberton et al., 1996:210. Emberton, 1997:1147. Emberton et al., 1999:table 2.

**Holotype:** USNM 860781 (ex MBI 373.02DH, adult shell).

**Paratypes:** MBI 373.02AP (1 ad [dissected]), MBI 374.10DP (1 ad), MBI 374.10AP (2 ad [2 dissected]), MBI 382.09DP (0; AMS C.203428 [1 ad]).

**Type locality:** Madagascar: Tulear Province: north of Fort Dauphin: northeast of village of Esetra: summit of Mount Mahermana, 340 m elevation: latitude 24°26'12"S, longitude 47°13'13"E: primary rainforest.

#### Description of holotype shell:

**Size and Shape.** Diameter 1.8 mm; height 2.2 mm. Height-diameter ratio 1.2. Spire angle 80 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 6% of shell diameter. Final umbilicus 13% of shell diameter. Whorls 4.2.

**Aperture.** Aperture width parallel to parietal callus 32% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 1.17. Columellar plica absent. Apertural plane inclined downward; 40 degrees from rotational axis. No apertural anal notch. Baso-columellar denticle present; size 15% of apertural width; depth 0.10 whorl. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest

width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 1.63. Aperture plus peristome greatest dimension angled outward from rotational axis 45 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 1.03. Peristome baso-palatal indentation 55% of basal peristome width. No peristome upper curl forward extension. Inner, second peristome absent.

**Apex.** Embryonic whorls 2.0. Embryonic sculpture smooth. First whorl diameter 0.42 mm. First three whorls diameter 1.24 mm.

**Sculpture on Last Tenth of Penultimate Whorl.** No transverse ribs. No complete spiral grooves between sutures. Eighteen short spiral grooves between sutures; short spiral grooves 0.06 mm long. No spiral ridges between sutures. No spiral lines of punctae between sutures. No herringbone sculpture; no honeycomb sculpture.

**Pre-Apertural Morphology.** Body whorl constricted 0.4 whorl before aperture; constricting by 22% of whorl diameter. Body whorl sculpture diminishes 70% before constriction. Post-constriction body whorl swollen by 24% of constriction diameter. Secondary body whorl constriction present; swelling after secondary constriction enlarged by 57% of diameter of first constriction. Transverse ribs on post-constrictional swelling numbering 9 in 0.1 whorl; rib height 1.1% of shell diameter; ribs not slanted.

**Color.** Basic color brown. Apex brown. No spiral color bands. Pre-apertural constriction brown. Peristome (excluding periostracum) brown.

**Shell variation:** The adult from station MBI-374 is much smaller than the holotype: height 2.0 mm.

**Shell comparisons:** Most similar to *Boucardicus clarea* Emberton, 1994, which however lacks the sculpture and the great preapertural swelling of this species, and which has a much more trilobed peristome.

**Description of reproductive characters (MBI 373.02AP: 1 female; MBI 374.10AP: 1 male, 1 female):** Penis length 1.4 mm, 0.8 shell diameter. Penial papilla-ejaculatory-pore position dorsal. Penial dorsal papilla absent. Penis terminal swelling conspicuous, terminal-bulb width 1.4 pre-bulb width. Penial gland absent. Base of FPSC (fertilization pouch-seminal receptacle complex) narrow-based, unlobed. Ducted gland on base of FPSC present. Muscular funnel within body of FPSC absent. Body-and-tube shape of FPSC: upper mid-body folded left, apex-plus-tube a squashed, backward "S."

**Distribution:** Found on Mts. Mahermana and Vasiha, from 300 to 860 m elevation. Also reported (Emberton, in press) from Mt. Teloboko, near Mahermana; from Andohahela (400–1100 m) and Beampingaratra in the Anosy Chain (380–500 m); and from Mount Ramabeafo (300–560 m), which runs between the southern Anosy and Vohimena Chains; but nowhere else. Thus a species





## Explanation of Figures 11–13

Shells of Mahermana-Iapiry-vasiha *Boucardicus*. Figure 11. *Boucardicus tridentatus* Emberton & Pearce, sp. nov., juvenile paratype. Figure 12. *Boucardicus rakotoarisoni* Emberton & Pearce, sp. nov., holotype. Figure 13. *Boucardicus simplex* Emberton & Pearce, sp. nov., holotype. All scale bars 1 mm.

of higher elevations (300+ m) that ranges throughout the Anosy Chain with extensions into the northern Vohimana Chain and toward but not into the southern Vohimana Chain. Thus *Boucardicus rakotoarisoni* occurs in fragmented populations within less than 1000 km<sup>2</sup> of declining forest, so meets criteria (IUCN, 1996) for Endangered status.

**Etymology:** For Jean Marcel Rakotoarison of the Rano-mafana National Park Project, former student and skilled associate in both field and lab, who has collected extensively on Andohahela.

*Boucardicus simplex* Emberton & Pearce, sp. nov.

(Figure 13)

*Boucardicus* sp. 11, Emberton et al., 1996:210. Emberton, 1997:1146, 1149. Emberton et al., 1999:table 2.

**Holotype:** USNM 860782 (ex MBI 377.01DH, adult shell).

**Paratypes:** MBI 377.01DP (2 ad, 3 juv; AMS C.203429 [1 ad]; MNHN [1 ad]; ANSP 400826 [1 ad]), 378.10DP (1 ad), MBI 379.12DP (2 juv).

**Type locality:** Madagascar: Tulear Province: north of Fort Dauphin: west of village of Mahialambo: summit of Mount Ilapiry, 540 m elevation: latitude 24°51'40"S, longitude 47°00'20"E: primary rainforest.

#### Description of holotype shell:

*Size and Shape.* Diameter 3.6 mm; height 4.2 mm. Height-diameter ratio 1.2. Spire angle 65 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 4% of shell diameter. Final umbilicus 6% of shell diameter. Whorls 5.6.

*Aperture.* Aperture width parallel to parietal callus 42% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 0.95. Columellar plica absent. Apertural plane inclined downward; 10 degrees from rotational axis. No apertural anal notch. No baso-columellar denticle. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 1.18. Aperture plus peristome greatest dimension angled outward from rotational axis 35 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 0.90. No peristome baso-palatal indentation. No peristome upper curl forward extension. Inner, second peristome absent.

*Apex.* Embryonic whorls 1.5. Embryonic sculpture smooth. First whorl diameter 0.45 mm. First three whorls diameter 1.13 mm.

*Sculpture on Last Tenth of Penultimate Whorl.* Transverse ribs 24; rib height less than 0.05% of shell diameter. No complete spiral grooves between sutures. No short spiral grooves between sutures. No spiral ridges between

sutures. Seventeen spiral lines of punctae between sutures; spiral lines of punctae numbering 24 per 0.1 whorl. No herringbone sculpture; no honeycomb sculpture.

*Pre-Apertural Morphology.* Body whorl constricted 0.1 whorl before aperture; constricting by 1% of whorl diameter. Body whorl sculpture not diminishing before constriction. Post-constriction body whorl swollen by 1% of constriction diameter. No secondary body whorl constriction. Transverse ribs on post-constrictional swelling numbering 18 in 0.1 whorl; rib height less than 0.05% of shell diameter; ribs not slanted.

*Color.* Basic color yellow. Apex yellow. No spiral color bands. Pre-apertural constriction red-brown. Peristome (excluding periostracum) white.

**Shell variation:** The five adult dry shells from MBI-377 range in height from 3.0 to 4.1 mm.

**Shell comparisons:** Much smaller and more acutely spired than *Boucardicus soulaianus* Fischer-Piette, Blanc, Blanc & Salvat, 1993. Smaller aperture and more acutely spired than *B. peani* Fischer-Piette, Blanc, Blanc & Salvat, 1993.

**Reproductive characters:** Unknown.

**Distribution:** Found only on Mt. Ilapiry, from only 400 to 540 m elevation. Not known from any other localities (Emberton, in press). A Critically Endangered species, by IUCN (1996) criteria, because its extent of occurrence is much less than 100 km<sup>2</sup>, it is known from just a single location, and slash-and-burn agriculture is continually destroying its habitat.

**Etymology:** For the relatively simple (*L. simplex*) shape of the shell.

*Boucardicus fortistriatus* Emberton & Pearce, sp. nov.

(Figure 14)

*Boucardicus* sp. 12, Emberton et al., 1996:210. Emberton, 1997:1147. Emberton et al., 1999:table 2.

**Holotype:** USNM 860783 (ex MBI 382.02DH, adult shell).

**Paratypes:** MBI 382.02DP (0; AMS C.203430 [1 ad]).

**Type locality:** Madagascar: Tulear Province: northwest of Fort Dauphin: west of village of Malio: local summit of Mount Vasiha, south of main summit, 860 m elevation: latitude 24°55'18"S, longitude 46°44'19"E: primary rainforest.

#### Description of holotype shell:

*Size and Shape.* Diameter 2.1 mm; height 2.3 mm. Height-diameter ratio 1.1. Spire angle 80 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 2% of shell diameter. Final umbilicus 12% of shell diameter. Whorls 4.4.





## Explanation of Figures 14–16

Shells of Mahermana-Ilapiry-Vasiha *Boucardicus*. Figure 14. *Boucardicus fortistriatus* Emberton & Pearce, sp. nov., holotype. Figure 15. *Boucardicus mahermanae* Emberton & Pearce, sp. nov., holotype. Figure 16. *Boucardicus carylae* Emberton & Pearce, sp. nov., holotype. All scale bars 1 mm.

**Aperture.** Aperture width parallel to parietal callus 38% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 0.89. Columellar plica absent. Apertural plane inclined downward; 30 degrees from rotational axis. No apertural anal notch. No baso-columellar denticle. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 1.44. Aperture plus peristome greatest dimension angled outward from rotational axis 40 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 1.31. Peristome baso-palatal indentation 20% of basal peristome width. No peristome upper curl forward extension. Inner, second peristome absent.

**Apex.** Embryonic whorls 1.6. Embryonic sculpture smooth. First whorl diameter 0.40 mm. First three whorls diameter 1.28 mm.

**Sculpture on Last Tenth of Penultimate Whorl.** No transverse ribs. No complete spiral grooves between sutures. No short spiral grooves between sutures. Nineteen spiral ridges between sutures; spiral ridges 1.00 mm high; spiral ridges not wavy. No spiral lines of punctae between sutures. No herringbone sculpture; no honeycomb sculpture.

**Pre-Apertural Morphology.** Body whorl constricted 0.2 whorl before aperture; constricting by 13% of whorl diameter. Body whorl sculpture not diminishing before constriction. Post-constriction body whorl swollen by 22% of constriction diameter. Secondary body whorl constriction present; swelling after secondary constriction enlarged by 30% of diameter of first constriction. Transverse ribs on post-constrictional swelling numbering 11 in 0.1 whorl; rib height 1.0% of shell diameter; ribs slanting backward; 10 degrees.

**Color.** Basic color brown-red. Apex brown-red. No spiral color bands. Pre-apertural constriction brown-red. Peristome (excluding periostracum) brown-red.

**Shell comparisons:** Unique for its strong spiral sculpture and compact, simple shape.

**Reproductive characters:** Unknown.

**Distribution:** Known only from Mt. Vasiha, on a local summit of 860 m elevation. Not known from any other localities (Emberton, in press). Like the above species, *Boucardicus fortistriatus* sp. nov. is Critically Endangered by IUCN (1996) criteria, because its extent of occurrence is much less than 100 km<sup>2</sup>, it is known from just a single location, and slash-and-burn agriculture is continually eroding its habitat.

**Etymology:** For the sculpture of strong (*L. forti-*) spiral grooves (*L. striatus*).

*Boucardicus mahermanae* Emberton & Pearce,  
sp. nov.

(Figures 15, 44, 65)

*Boucardicus* sp. 13, Emberton et al., 1996:210. Emberton, 1997:1146, 1149. Emberton et al., 1999:table 2.

**Holotype:** USNM 860784 (ex MBI 373.03DH, adult shell).

**Paratypes:** MBI 373.03DP (1 juv; AMS C.203431 [1 ad]), MBI 373.03AP (7 ad [2 dissected]), MBI 374.24AP (3 ad), MBI 376.21AP (1 ad), MBI 380.25AP (1 juv).

**Type locality:** Madagascar: Tulear Province: north of Fort Dauphin: northeast of village of Esetra: summit of Mount Mahermana, 340 m elevation; latitude 24°26'12"S, longitude 47°13'13"E: primary rainforest.

#### Description of holotype shell:

**Size and Shape.** Diameter 3.2 mm; height 3.0 mm. Height-diameter ratio 0.9. Spire angle 70 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 4% of shell diameter. Final umbilicus 19% of shell diameter. Whorls 4.2.

**Aperture.** Aperture width parallel to parietal callus 28% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 0.96. Columellar plica absent. Apertural plane inclined upward; 5 degrees from rotational axis. Apertural anal notch 7% of apertural width. No baso-columellar denticle. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 2.11. Aperture plus peristome greatest dimension angled outward from rotational axis 30 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 1.29. Peristome baso-palatal indentation 44% of basal peristome width. Peristome upper curl extends forward 100% of upper peristome width. Inner, second peristome present, projecting more than 0.01 whorl.

**Apex.** Embryonic whorls 1.9. Embryonic sculpture smooth. First whorl diameter 0.63 mm. First three whorls diameter 1.73 mm.

**Sculpture on Last Tenth of Penultimate Whorl.** No transverse ribs. No complete spiral grooves between sutures. No short spiral grooves between sutures. No spiral ridges between sutures. No spiral lines of punctae between sutures. No herringbone sculpture; no honeycomb sculpture.

**Pre-Apertural Morphology.** Body whorl constricted 0.5 whorl before aperture; constricting by 12% of whorl diameter. Body whorl sculpture not diminishing before constriction. Post-constriction body whorl swollen by 12% of constriction diameter. Secondary body whorl constriction present; swelling after secondary constriction enlarged by 27% of diameter of first constriction. Transverse ribs on



post-constrictional swelling numbering 12 in 0.1 whorl; rib height 1.6% of shell diameter; ribs slanting forward; 30 degrees.

**Color.** Basic color brown-red. Apex brown-red. Two spiral color bands; color white. Pre-apertural constriction brown-red. Peristome (excluding periostracum) red-brown and white.

**Shell comparisons:** Most similar to *Boucardicus andringitrae* Fischer-Piette, Blanc, Blanc & Salvat, 1993, but without severe swellings and apertural dentition, and with a robust upper forward extension of the peristome.

**Description of reproductive characters (MBI 373.03AP: 1 male, 1 female):** Penis length 2.7 mm, 0.8 shell diameter. Penial papilla-ejaculatory-pore position dorsal. Penial dorsal papilla terminal, weak to no protrusion beyond tip of penis, anteriorly directed. Penis terminal swelling slight, terminal-bulb width 1.2 pre-bulb width. Penial gland present. Penial-gland length 1.4 penis pre-terminal-bulb width. Penial-gland position proximal, its center 0.4 along the penis length from its base. Penial-gland attachment position ventral. Penial-gland free lobe direction left. Base of FPSC (fertilization pouch-seminal receptacle complex) narrow-based, with two ovate apical lobes. Ducted gland on base of FPSC absent. Body-and-tube shape of FPSC: upper mid-body folded left, apex-plus-tube a squashed, backward "S."

**Distribution:** On both Vohimena-Chain mountains (Maherana and Ilapiry), from 100 to 340 m elevation. Also found in two patches of coastal forest just east of the Vohimena Chain (Ste. Luce and 4.6 km south of Manambato), and found in the near-coastal forest (elevation ca. 50 m) of Manombo, but nowhere else (Emberton, in press). Thus, restricted to lowland coastal forest between Manombo (some 33 km south of Farafangana) and Mount Ilapiry. This forest is continually diminishing and/or degrading and extends much less than 5000 km<sup>2</sup>. *Boucardicus maheranae* sp. nov. is severely fragmented into subpopulations surviving in remnant patches of forest. By these criteria, it is an Endangered species (IUCN, 1996).

**Etymology:** For Mount Maherana, northern Vohimena Chain.

*Boucardicus carylae* Emberton & Pearce, sp. nov.  
(Figures 16, 45, 66)

*Boucardicus* sp. 14, Emberton et al., 1996:210. Emberton, 1997:1147. Emberton et al., 1999:table 2.

**Holotype:** USNM 860785 (ex MBI 377.02DH, adult shell).

**Paratypes:** MBI 377.02DP (1 ad, 2 juv; AMS C.203432 [1 ad]), MBI 377.02AP (6 ad), MBI 378.20AP (7 ad [1 dissected]), MBI 379.34AP (1 ad, 1 juv), MBI 382.10DP (1 ad), MBI 382.10AP (2 ad [1 dissected]).

**Type locality:** Madagascar: Tulear Province: north of Fort Dauphin: west of village of Mahialambo: summit of Mount Ilapiry, 540 m elevation: latitude 24°51'40"S, longitude 47°00'20"E: primary rainforest.

#### Description of holotype shell:

**Size and Shape.** Diameter 1.5 mm; height 1.7 mm. Height-diameter ratio 1.1. Spire angle 65 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 2% of shell diameter. Final umbilicus 9% of shell diameter. Whorls 4.4.

**Aperture.** Aperture width parallel to parietal callus 34% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 0.95. Columellar plica absent. Apertural plane inclined upward; 15 degrees from rotational axis. Apertural anal notch 7% of apertural width. No baso-columellar denticle. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 1.68. Aperture plus peristome greatest dimension angled outward from rotational axis 25 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 1.42. Peristome baso-palatal indentation 83% of basal peristome width. Peristome upper curl extends forward 33% of upper peristome width. Inner, second peristome present, projecting less than 0.01 whorl.

**Apex.** Embryonic whorls 1.8. Embryonic sculpture smooth. First whorl diameter 0.29 mm. First three whorls diameter 0.78 mm.

**Sculpture on Last Tenth of Penultimate Whorl.** Transverse ribs 12; rib height 0.7% of shell diameter. No complete spiral grooves between sutures. No short spiral grooves between sutures. No spiral ridges between sutures. No spiral lines of punctae between sutures. No heringbone sculpture; no honeycomb sculpture.

**Pre-Apertural Morphology.** Body whorl constricted 0.1 whorl before aperture; constricting by 16% of whorl diameter. Body whorl sculpture diminishes 50% before constriction. Post-constriction body whorl swollen by 32% of constriction diameter. No secondary body whorl constriction. Transverse ribs on post-constrictional swelling numbering 9 in 0.1 whorl; rib height 0.7% of shell diameter; ribs not slanted.

**Color.** Basic color yellow-brown. Apex yellow-brown. No spiral color bands. Pre-apertural constriction yellow-brown. Peristome (excluding periostracum) yellow-brown.

**Shell variation:** No conspicuous variation in size or shape.

**Shell comparisons:** Unique in its combination of ribbed overall sculpture, post-constriction swelling that is extreme and close to the aperture, and upper outer peristome that flares broadly at and adherent to the body whorl.

**Description of reproductive characters (MBI 378.20AP: 1 male; MBI 382.10AP: 1 female):** Penis length 0.9 mm, 0.6 shell diameter. Penial papilla-ejaculatory-pore position central. Penis terminal swelling slight, terminal-bulb width 1.1 pre-bulb width. Penial gland absent. Base of FPSC (fertilization pouch-seminal receptacle complex) narrow-based, with multiple apical lobes. Ducted gland on base of FPSC absent. Body-and-tube shape of FPSC: upper body bent right and downward, apex-plus-tube an up-pointed "U."

**Distribution:** Mts. Ilapiry and Vasiha, 540–860 m elevation. Also found on Andohahela, 800–1900 m; but nowhere else (Emberton, in press). Its range, therefore, seems restricted to the southern Anosy and Vohimena Chains, and extends less than 1000 km<sup>2</sup>. Its area and quality of habitat are under continuing decline, and its distribution is severely fragmented by its apparent restriction to high elevations (500+ m). Therefore *Boucardicus carylae* sp. nov. is an Endangered species by IUCN (1996) criteria.

**Etymology:** For Caryl Hesterman, in grateful recognition of her former service as Secretary-Treasurer of the Moluscan Biodiversity Institute.

*Boucardicus magnilobatus* Emberton & Pearce,  
sp. nov.

(Figure 17)

*Boucardicus* n. sp. 27, in part, Emberton, 1996:735.

*Boucardicus* sp. 15, Emberton et al., 1996:210. Emberton, 1997:1147. Emberton et al., 1999:table 2.

**Holotype:** USNM 860786 (ex MBI 378.01DH, adult shell).

**Paratypes:** None.

**Type locality:** Madagascar: Tulear Province: north of Fort Dauphin: west of village of Mahialambo: east-facing ridge of Mount Ilapiry, 500 m elevation: latitude 24°51'33"S, longitude 47°00'27"E: primary rainforest.

#### Description of holotype shell:

**Size and Shape.** Diameter 2.1 mm; height 3.0 mm. Height-diameter ratio 1.4. Spire angle 70 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 3% of shell diameter. Final umbilicus 10% of shell diameter. Whorls 4.3.

**Aperture.** Aperture width parallel to parietal callus 35% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 1.19. Columellar plica absent. Apertural plane inclined downward; 50 degrees from rotational axis. No apertural anal notch. No baso-columellar denticle. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 1.21. Aperture plus

peristome greatest dimension angled outward from rotational axis 90 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 0.82. Peristome baso-palatal indentation 43% of basal peristome width. No peristome upper curl forward extension. Inner, second peristome present, projecting less than 0.01 whorl.

**Apex.** Embryonic whorls 1.7. Embryonic sculpture smooth. First whorl diameter 0.56 mm. First three whorls diameter 1.54 mm.

**Sculpture on Last Tenth of Penultimate Whorl.** No transverse ribs. No complete spiral grooves between sutures. No short spiral grooves between sutures. No spiral ridges between sutures. No spiral lines of punctae between sutures. No herringbone sculpture; no honeycomb sculpture.

**Pre-Apertural Morphology.** Body whorl constricted 0.6 whorl before aperture; constricting by 22% of whorl diameter. Body whorl sculpture not diminishing before constriction. Post-constriction body whorl swollen by 64% of constriction diameter. Secondary body whorl constriction present; swelling after secondary constriction enlarged by 100% of diameter of first constriction. Transverse ribs on post-constrictional swelling numbering 9 in 0.1 whorl; rib height 1.9% of shell diameter; ribs slanting forward; 50 degrees.

**Color.** Basic color brown. Apex brown. No spiral color bands. Pre-apertural constriction brown. Peristome (excluding periostracum) brown.

**Shell comparisons:** Most similar to *Boucardicus seguini* Fischer-Piette, Blanc, Blanc & Salvat, 1993, but with a much earlier preapertural constriction of the body whorl, a greater preapertural swelling, and a more triangular aperture.

**Reproductive characters:** Unknown.

**Distribution:** Mt. Ilapiry at 500 m elevation. Emberton (in press) also gives localities from Andohahela (430–1400 m), Col Beampingaratra (600–800 m), and Mt. Ramabeafo (580–700 m). Thus with a range in the Anosy and southern Vohimena Chains. An Endangered species by IUCN (1996) criteria because of its small range (< 1000 km<sup>2</sup>), decline in area and quality of habitat, and extreme fragmentation into high-elevation "islands" of forest.

**Etymology:** For the large (*L. magni*-) lobelike preapertural swelling (*L. lobatus*) of the body whorl.

*Boucardicus fidimananai* Emberton & Pearce,  
sp. nov.

(Figure 18)

*Boucardicus* sp. 16, Emberton et al., 1996:210. Emberton, 1997:1147. Emberton et al., 1999:table 2.





## Explanation of Figures 17–19

Shells of Mahermana-Ilapiry-Vasiha *Boucardicus*. Figure 17. *Boucardicus magnilobatus* Emberton & Pearce, sp. nov., holotype. Figure 18. *Boucardicus fidimananai* Emberton & Pearce, sp. nov., holotype. Figure 19. *Boucardicus randalanai* Emberton & Pearce, sp. nov., holotype. All scale bars 1 mm.

**Holotype:** USNM 860787 (ex MBI 378.02DH, adult shell).

**Paratypes:** MBI 378.02AP (1 juv).

**Type locality:** Madagascar: Tulear Province: north of Fort Dauphin: west of village of Mahialambo: east-facing ridge of Mount Ilapiry, 500 m elevation: latitude 24°51'33"S, longitude 47°00'27"E: primary rainforest.

**Description of holotype shell:**

*Size and Shape.* Diameter 3.3 mm; height 3.9 mm. Height-diameter ratio 1.2. Spire angle 75 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 3% of shell diameter. Final umbilicus 12% of shell diameter. Whorls 4.5.

*Aperture.* Aperture width parallel to parietal callus 43% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 0.89. Columellar plica absent. Apertural plane parallel to rotational axis. No apertural anal notch. No baso-columellar denticle. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 1.11. Aperture plus peristome greatest dimension angled outward from rotational axis 55 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 1.14. No peristome baso-palatal indentation. No peristome upper curl forward extension. Inner, second peristome absent.

*Apex.* Embryonic whorls 2.0. Embryonic sculpture granular. First whorl diameter 0.65 mm. First three whorls diameter 1.91 mm.

*Sculpture on Last Tenth of Penultimate Whorl.* No transverse ribs. No complete spiral grooves between sutures. No short spiral grooves between sutures. No spiral ridges between sutures. No spiral lines of punctae between sutures. No herringbone sculpture; no honeycomb sculpture.

*Pre-Apertural Morphology.* Body whorl constricted 0.1 whorl before aperture; constricting by 2% of whorl diameter. Lack of body whorl sculpture continues into constriction. Post-constriction body whorl swollen by 9% of constriction diameter. No secondary body whorl constriction. Transverse ribs on post-constrictional swelling numbering 18 in 0.1 whorl; rib height 1.8% of shell diameter; ribs slanting forward; 70 degrees.

*Color.* Basic color brown-red. Apex brown-red. No spiral color bands. Pre-apertural constriction brown-red.

**Shell comparisons:** Smaller and squatter than *Boucardicus peani* Fischer-Piette, Blanc, Blanc & Salvat, 1993, and without its spiral sculpture.

**Reproductive characters:** Unknown.

**Local distribution:** Known only from Mt. Ilapiry at 500 m elevation. Not reported from any other locality (Em-

berton, in press). Therefore a Critically Endangered species by IUCN (1996) criteria, occurring in much less than 100 km<sup>2</sup> of continually declining and degrading forest.

**Etymology:** For Fidimanana, able lab and field assistant, and dedicated student of malacology.

*Boucardicus randalanai* Emberton & Pearce,  
sp. nov.

(Figure 19)

*Boucardicus* n. sp. 28, in part, Emberton, 1996:735.

*Boucardicus* sp. 17, Emberton et al., 1996:210. Emberton, 1997:1147. Emberton et al., 1999:table 2.

**Holotype:** USNM 860788 (ex MBI 373.04DH, adult shell).

**Paratypes:** MBI 373.04AP (1 juv).

**Type locality:** Madagascar: Tulear Province: north of Fort Dauphin: northeast of village of Esetra: summit of Mount Mahermana, 340 m elevation: latitude 24°26'12"S, longitude 47°13'13"E: primary rainforest.

**Description of holotype shell:**

*Size and Shape.* Diameter 1.4 mm; height 2.1 mm. Height-diameter ratio 1.4. Spire angle 70 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 9% of shell diameter. Final umbilicus 11% of shell diameter. Whorls 5.0.

*Aperture.* Aperture width parallel to parietal callus 39% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 1.00. Columellar plica absent. Apertural plane inclined downward; 5 degrees from rotational axis. No apertural anal notch. Baso-columellar denticle present; size 9% of apertural width; depth 0.00 whorl. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 1.36. Aperture plus peristome greatest dimension angled outward from rotational axis 50 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 1.06. Peristome baso-palatal indentation 29% of basal peristome width. No peristome upper curl forward extension. Inner, second peristome absent.

*Apex.* Embryonic whorls 1.9. Embryonic sculpture smooth. First whorl diameter 0.38 mm. First three whorls diameter 0.95 mm.

*Sculpture on Last Tenth of Penultimate Whorl.* Transverse ribs 80; rib height 0.7% of shell diameter. No complete spiral grooves between sutures. No short spiral grooves between sutures. No spiral ridges between sutures. No spiral lines of punctae between sutures. No herringbone sculpture; 28 honeycombs.

*Pre-Apertural Morphology.* Body whorl constricted 0.1 whorl before aperture; constricting by less than 0.5% of



whorl diameter. Body whorl sculpture not diminishing before constriction. Post-constriction body whorl swollen by 20% of constriction diameter. No secondary body whorl constriction. Transverse ribs on post-constrictional swelling numbering 9 in 0.1 whorl; rib height 0.7% of shell diameter; ribs slanting forward; 80 degrees.

**Color.** Basic color yellow. Apex brown. No spiral color bands. Pre-apertural constriction yellow. Peristome (excluding periostracum) yellow.

**Shell comparisons:** Unique in its honeycomb sculpture. Most similar, in its minute, high-spined shell, to *Boucardicus delicatus* sp. nov., from which it differs in its larger, more circular aperture.

**Reproductive characters:** Unknown.

**Distribution:** The summit of Mt. Mahermana, 340 m elevation. Also found at high elevation (530 m) on the adjacent Mt. Teloboko, but nowhere else (Emberton, in press). This species is fragmented into two isolated subpopulations that occupy < 10 km<sup>2</sup> of forest that is succumbing rapidly to logging and slash-and-burn agriculture. It meets criteria of the IUCN (1996) for Critically Endangered status.

**Etymology:** For Roger Randalana, former student and able associate in field and lab.

Genus *Cyathopoma* W. & H. Blanford, 1861

*Cyathopoma randalana* Emberton & Pearce,  
sp. nov.

(Figures 20, 21, 31, 46, 67)

*Cyathopoma* sp. 1, Emberton et al., 1996:210. Emberton, 1997:1146, 1149.

**Holotype:** USNM 860789 (ex MBI 379.01DH, adult shell).

**Paratypes:** MBI 373.15DP (2 ad, 2 juv), MBI 373.15AP (1 ad), MBI 374.11DP (1 ad), MBI 374.11AP (1 ad), MBI 375.09DP (2 juv), MBI 375.09AP (2 ad [1 dissected], 3 juv), MBI 376.07DP (4 ad), MBI 376.07AP (3 ad [1 dissected]), MBI 377.22AP (1 ad, 1 juv), MBI 378.11DP (1 juv), MBI 379.01DP (4 ad, 1 juv; AMS C.203433 [1 ad]; MNHN [1 ad]; ANSP 400827 [1 ad]), MBI 379.01AP (3 ad), MBI 380.10DP (1 ad), MBI 383.07DP (2 ad, 1 juv), MBI 383.07AP (1 juv), MBI 391.04AP (1 ad).

**Type locality:** Madagascar: Tulear Province: north of Fort Dauphin: west of village of Mahialambo: SSE-facing side of Mount Ilapiry, 400 m elevation: latitude 24°51'27"S, longitude 47°00'38"E: primary rainforest.

#### Description of holotype shell:

**Size and Shape.** Shell dextral. Diameter 2.0 mm; height 2.0 mm. Height-diameter ratio 1.0. Whorls 4.3. Spire angle 85 degrees. Apex angle 90 degrees. Spire profile convexity (outward departure from a straight line tangent to

whorls n-0.5 and about the second whorl). 1% of shell diameter. Whorl periphery round. Suture depth one half whorl from aperture is 5% of shell diameter. Final umbilicus 20% of shell diameter. Coiling tightness (whorl number divided by natural logarithm of shell diameter) 6.2. Operculum concentric with five ridges of concentric thin lamellae.

**Aperture.** Aperture width (inside dimension, parallel to a line between the columellar and upper peristome insertions) 40% of shell diameter. Aperture height-width ratio (inside dimension, height measured to and perpendicular to a line between the columellar and upper peristome insertions) 0.91. Distance between columellar and upper peristome insertions is 44% of aperture width. Penultimate whorl not projecting into body whorl. Columella not truncate. Columellar plica absent. Columella not reflected. Apertural plane inclined downward; 5 degrees from rotational axis. Aperture shape circular, outer aperture with a slightly forwardly projecting curl at its baso-columellar edge. Peristome reflected; second, internal peristome present, projecting more than 0.01 whorl. Ratio of aperture width including peristome to aperture width excluding peristome 1.3. Change in growth direction of body whorl; occurs 0.2 whorls behind aperture. Apertural dentition absent.

**Apex.** Embryonic whorls 1.7; diameter 0.6 mm. First whorl diameter 0.4 mm. First two whorls diameter 0.7 mm. Embryonic whorls smooth.

**Post-Embryonic Shell Sculpture and Color.** Post-embryonic shell with extremely fine, crowded transverse grooves; upper suture canaliculate by a ridge of periostracum only; top of whorl shoulder with transverse grooves only, then between outer edge of whorl shoulder and the lower suture are five strong spiral ridges. Spiral ridge sculpture continues on shell base and into umbilicus and is unchanged at end of growth near aperture. Basic shell color white.

**Shell variation:** There is great variation in size, both within and among populations. Figures 20 and 21 contrast a small specimen (Figure 20) with a large (Figure 21; note difference in scale bars).

**Shell comparisons:** Most similar to *Cyathopoma filocinctum* Benson, 1851, but much smaller for the same number of whorls.

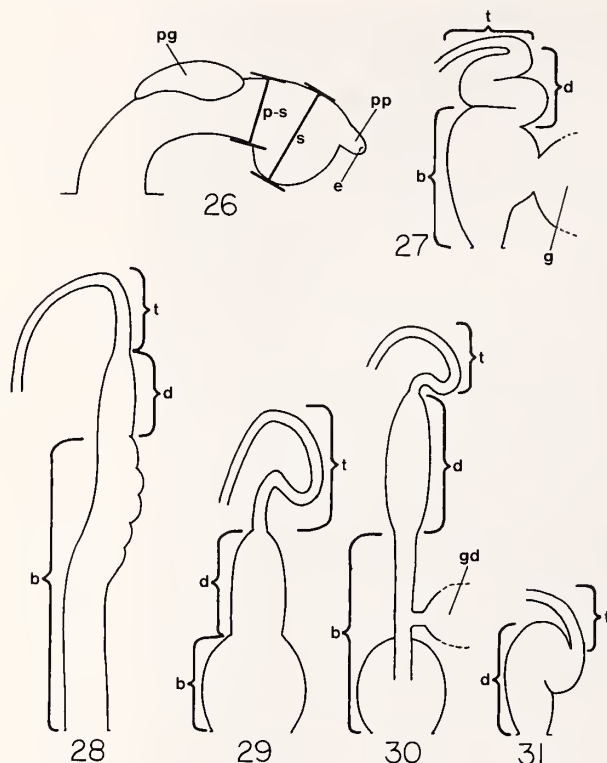
**Description of reproductive characters (MBI 375.09AP: 1 female; MBI 376.07AP: 1 male):** Penis length 1.2 mm, 0.6 shell diameter. Penial papilla-ejaculatory-pore position central. Penis terminal swelling conspicuous, terminal-bulb width 1.3 pre-bulb width. Penial gland absent. Base of FPSC (fertilization pouch-seminal receptacle complex) undetectable. Ducted gland on base of FPSC absent. Body-and-tube shape of FPSC: upper body folded right and downward, apex-plus-tube an up-pointed "V."



Explanation of Figures 20–25

Shells of other small Mahermana-Ilapiry-Vasiha caenogastropods. Figures 20–21. *Cyathopoma randalana*, Emberton & Pearce, sp. nov., representatives from Mounts Mahermana (Figure 20) and Ilapiry (Figure 21). Figure 22. *Malarinia calcopercula* Emberton, 1994, representative from Mount Ilapiry. Figure 23. *Tropidophora (Ligatella) vallorzi* Fischer-Piette, Blanc, Blanc & Salvat, 1993, representative from Mount Vasiha. Figure 24. *Omphalotropis vohimenae* Emberton & Pearce, sp. nov., holotype. Figure 25. *Omphalotropis costulata* Emberton & Pearce, sp. nov., holotype. All scale bars 1 mm.





Explanation of Figures 26–31

Some reproductive characters (Table 1) used in descriptions, as shown on stylized penis (Figure 26) and five types of FPSC (fertilization pouch-seminal receptacle complex; Figures 27–31). Abbreviations: b, base (glandular) of FPSC; d, body of FPSC; e, ejaculatory pore of penis; g, gland of FPSC; gd, ducted gland of FPSC; p-s, pre-swelling width of penis; pg, penial gland; pp, penial papilla; s, swelling width of penis; t, tube of FPSC. Stylized FPSCs: Figure 27, *Boucardicus rakotoarisoni* Emberton & Pearce, sp. nov.; Figure 28, *B. albocinctus*; Figure 29, *B. esetrae* Emberton & Pearce, sp. nov.; Figure 30, *B. divei*; Figure 31, *Cyathopoma randalana* Emberton & Pearce, sp. nov.

**Local distribution:** All three mountains, 100–700 m elevation.

**Etymology:** Also for Roger Randalana, in grateful recognition of his unflagging assistance throughout the Tolagnaro project.

Genus *Hainesia* Pfeiffer, 1856

*Hainesia crocea* (Sowerby, 1847)

Family DIPLOMMATINIDAE

Genus *Malarinia* Haas, 1961

*Malarinia calcopercula* Emberton, 1994

(Figure 22)

*Malarinia* sp. 1, Emberton et al., 1996:210. Emberton, 1997: 1147.

**Representative:** MBI 380.01DR (ad).

**Other specimens:** None.

#### Description of representative shell:

**Size and Shape.** Shell dextral. Diameter 2.2 mm; height 4.6 mm. Height-diameter ratio 2.1. Whorls 5.5. Spire angle 35 degrees. Apex angle 50 degrees. Spire profile convexity (outward departure from a straight line tangent to whorls n-0.5 and about the second whorl); 11% of shell diameter. Whorl periphery round. Suture depth one half whorl from aperture is 6% of shell diameter. Umbilicus before change in body whorl growth direction 3% of shell diameter. Final umbilicus 6% of shell diameter. Coiling tightness (whorl number divided by natural logarithm of shell diameter) 7.0.

**Aperture.** Aperture width (inside dimension, parallel to a line between the columellar and upper peristome insertions) 49% of shell diameter. Aperture height-width ratio (inside dimension, height measured to and perpendicular to a line between the columellar and upper peristome insertions) 1.00. Distance between columellar and upper peristome insertions is 41% of aperture width. Penultimate whorl not projecting into body whorl. Columella not truncate. Columellar plica absent. Columella slightly reflected. Apertural plane inclined downward; 5 degrees from rotational axis. Aperture shape sub-circular. Peristome expanded and thickened internally; second, internal peristome present, projecting less than 0.01 whorl. Change in growth direction of body whorl; occurs 0.1 whorls behind aperture. Apertural dentition absent.

**Apex.** First whorl diameter 0.7 mm. First two whorls diameter 1.0 mm. Embryonic whorls eroded.

**Post-Embryonic Shell Sculpture and Color.** Post-embryonic shell with regularly spaced transverse ribs on lower half of penultimate whorl, becoming weak to absent on body whorl. Basic shell color light yellow-brown.

**Shell variation:** No conspicuous difference in size or shape from the holotype.

**Reproductive characters:** Unknown.

**Distribution:** Previously known only from Vato Vavy and Vato Lahy summits near Mananjary, ca. 500 m elevation (Emberton, 1994). This record from Mt. Ilapiry, 300 m elevation, is an extreme, southward range extension.

Superfamily LITTORINOIDEA

Family POMATIASIDAE

Genus *Tropidophora* Troschel, 1847

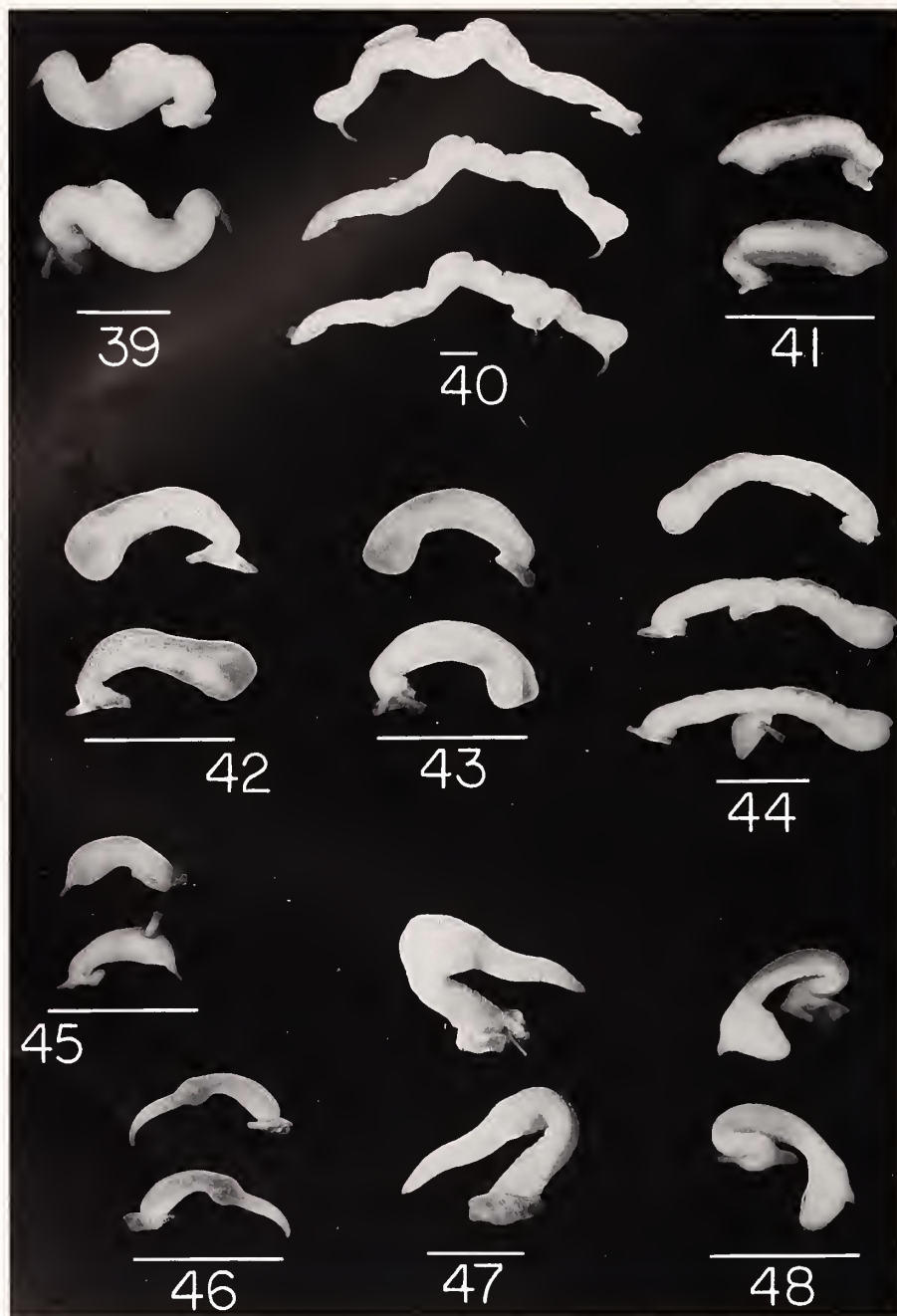
The large *Tropidophora* of Madagascar are currently in a taxonomic disorder that probably cannot be resolved without biochemical investigation (Emberton, 1995).



Explanation of Figures 32–38

Penes of Mahermana-Ilapiry-Vasiha *Boucardicus*. Figure 32. three stages in the dissection of a male to remove the penis (demonstrated on *Boucardicus albocinctus* [Smith, 1893]). Figure 33. *Boucardicus esetrae* Emberton & Pearce, sp. nov. Figure 34. *Boucardicus antiquus* Emberton & Pearce, sp. nov. Figure 35. *Boucardicus delicatus* Emberton & Pearce, sp. nov. Figure 36. *Boucardicus curvifolius* Emberton & Pearce, sp. nov. Figures 37–38. *Boucardicus albocinctus* (Smith, 1893): Figure 37, normal; Figure 38, mating. All scale bars 1 mm.





Explanation of Figures 39–48

Penes of Mahermana-Ilapiry-Vasiha *Boucardicus* and other small caenogastropods. Figure 39. *Boucardicus divei* Piette, Blanc, Blanc & Salvat, 1993. Figure 40. *Boucardicus culminans* Fischer-Piette, Blanc, Blanc & Salvat, 1993. Figure 41. *Boucardicus tridentatus* Emberton & Pearce, sp. nov. Figures 42–43. *Boucardicus rakotoarisoni* Emberton & Pearce, sp. nov., specimens from two populations. Figure 44. *Boucardicus mahermanae* Emberton & Pearce, sp. nov. Figure 45. *Boucardicus carylae* Emberton & Pearce, sp. nov. Figure 46. *Cyathopoma randalana* Emberton & Pearce, sp. nov. Figure 47. *Tropidophora (Ligatella) vallorzi* Fischer-Piette, Blanc, Blanc & Salvat, 1993. Figure 48. *Omphalotropis costulata* Emberton & Pearce, sp. nov. All scale bars 1 mm.

*Tropidophora* sp. 1*Tropidophora* sp. 2

*Tropidophora (Ligatella) vallorzi* Fischer-Piette,  
Blanc, Blanc & Salvat, 1993

(Figures 23, 47, 68)

*Tropidophora* sp. 1, Emberton et al., 1996:210. Emberton,  
1997:1146, 1149.

**Representative:** MBI 384.01DR (ad).

**Other specimens:** MBI 373.16D (3 ad, 9 juv), MBI 373.16A (2 ad, 7 juv), MBI 374.12D (4 juv), MBI 374.12A (3 ad, 2 juv), MBI 375.10D (2 ad, 9 juv), MBI 375.10A (3 ad, 3 juv), MBI 376.08D (3 ad, 11 juv), MBI 376.08A (1 ad, 4 juv), MBI 377.10D (2 ad, 7 juv), MBI 377.10A (3 juv), MBI 378.12D (12 juv), MBI 378.12A (1 ad, 7 juv), MBI 379.13D (6 ad, 13 juv), MBI 379.13A (4 juv), MBI 380.11D (3 ad, 15 juv), MBI 380.11A (11 juv), MBI 381.08D (3 ad, 20 juv), MBI 381.08A (2 ad [1 dissected], 18 juv), MBI 382.11D (1 juv), MBI 382.11A (2 juv), MBI 383.08D (4 ad, 17 juv), MBI 383.08A (4 juv), MBI 384.01D (6 ad, 21 juv; AMS C.203434 [1 ad]; MNHN [1 ad]; ANSP 400828 [1 ad]), MBI 384.01A (1 ad [dissected], 5 juv), MBI 385.05D (2 ad, 11 juv), MBI 385.05A (2 juv), MBI 386.08D (3 ad, 6 juv), MBI 386.08A (1 ad), MBI 387.05D (1 ad, 15 juv), MBI 387.05A (1 ad), MBI 388.03D (3 ad, 5 juv), MBI 391.01D (1 juv).

#### Description of representative shell:

**Size and Shape.** Shell dextral. Diameter 10.9 mm; height 12.2 mm. Height-diameter ratio 1.1. Whorls 4.9. Spire angle 70 degrees. Apex angle 70 degrees. Spire profile straight. Whorl periphery round. Suture depth one half whorl from aperture is 5% of shell diameter. Final umbilicus 8% of shell diameter. Coiling tightness (whorl number divided by natural logarithm of shell diameter) 2.0.

**Aperture.** Aperture width (inside dimension, parallel to a line between the columellar and upper peristome insertions) 47% of shell diameter. Aperture height-width ratio (inside dimension, height measured to and perpendicular to a line between the columellar and upper peristome insertions) 1.00. Distance between columellar and upper peristome insertions is 12% of aperture width. Penultimate whorl not projecting into body whorl. Columella not truncate. Columellar plica absent. Columella slightly reflected. Apertural plane inclined downward; 5 degrees from rotational axis. Aperture shape circular. Peristome reflected; no second, internal peristome. Ratio of aperture width including peristome to aperture width excluding peristome 1.2. No change in growth direction of body whorl near aperture. Apertural dentition absent.

**Apex.** First whorl diameter 1.4 mm. First two whorls diameter 2.2 mm. Embryonic whorls smooth.

**Post-Embryonic Shell Sculpture and Color.** Post-embryonic shell with four strong interrupted spiral ridges between sutures, white where they are strong, brown on both sides and where they are interrupted; with one weaker white spiral ridge between each stronger ridge on penultimate whorl, spiral ridges becoming more numerous on body whorl; sculpture continues on shell base and into umbilicus; frequent regular interruptions of spiral sculpture across the whorl extend as small ribs into the suture, and coincide with interruptions on the strong spiral ridges. Basic shell color light yellow-brown. Peristome (excluding periostracum) white with dark brown.

**Shell variation:** Most stations show a great dichotomy in size, presumably between males and females, as has been demonstrated for other *Tropidophora* (Emberton, 1995). The largest specimen reported here (station MBI 378) has 4.9 whorls, a diameter of 13.4 mm, and height of 14.8 mm. This specimen is also a uniform cream color, without darker color bands.

**Description of reproductive characters (MBI 384.01A: 1 male; MBI 381.08A: 1 female):** Penis length 5.2 mm, 0.5 shell diameter. Penial papilla-ejaculatory-pore position central. Penial papilla terminal, extremely strong protrusion, anteriorly directed. Penis terminal swelling slight. Penial gland absent. Base of FPSC (fertilization pouch-seminal receptacle complex) narrow-based, with multiple, internal apical lobes. Ducted gland on base of FPSC absent. Muscular funnel within body of FPSC apparently absent. Body-and-tube shape of FPSC: body-plus-tube sinuous, forming six loose, evenly spaced, "U" to "V" shaped bends.

**Distribution:** Described from the Anosy chain, Analava forest, and Ste. Luce forest (all north of Ft. Dauphin) (Fischer-Piette et al., 1993). Common throughout our samples on all three mountains, throughout all elevations (100–860 m).

**Comments:** It seems likely that *Tropidophora (Ligatella) maignei* Fischer-Piette, Blanc, Blanc & Salvat, 1993, is a synonym of this species.

### Superfamily RISSOOIDEA

#### Family ASSIMINEIDAE

#### Genus *Omphalotropis* Pfeiffer, 1851

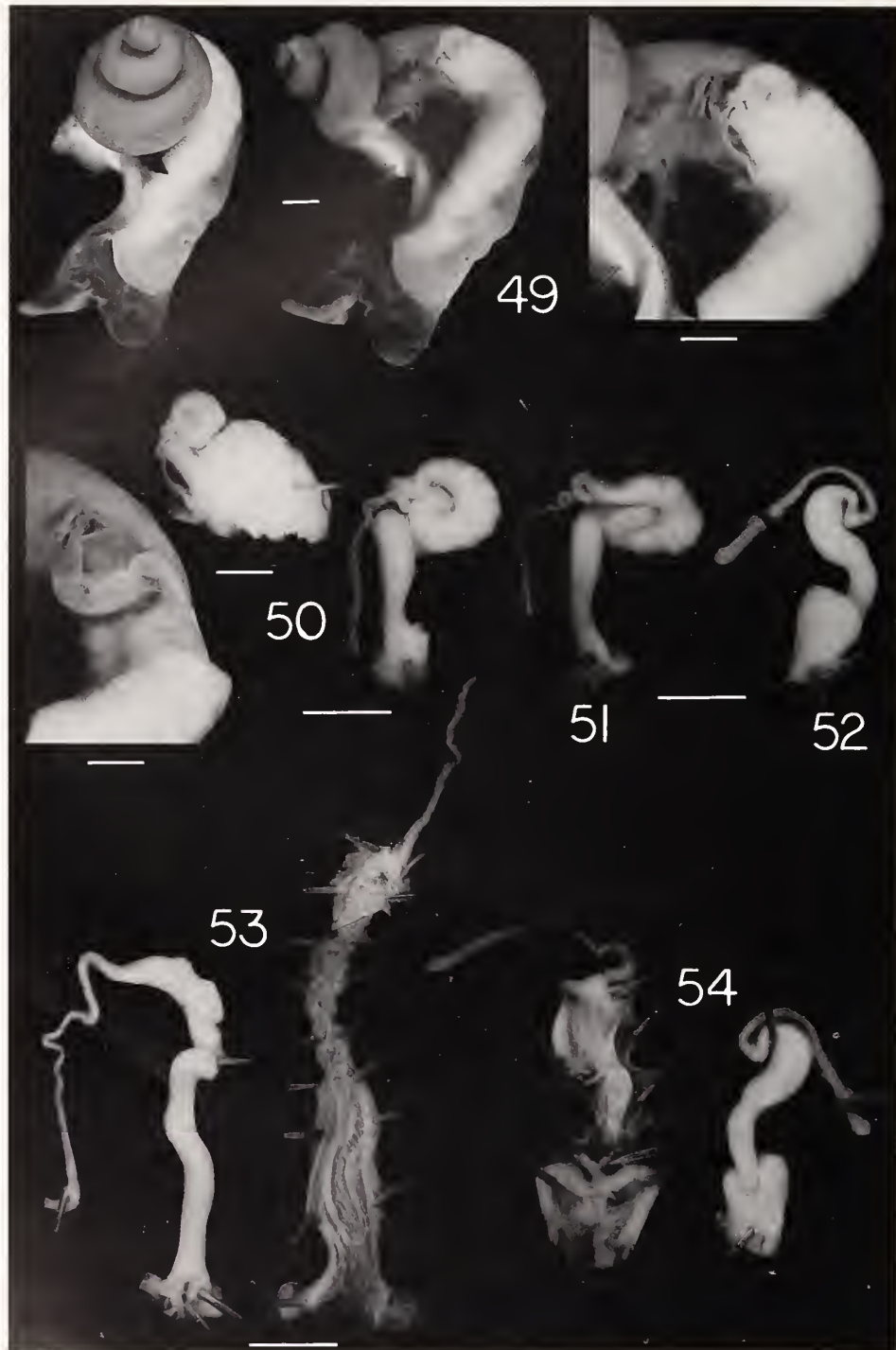
*Omphalotropis vohimenae* Emberton & Pearce,  
sp. nov.

(Figure 24)

*Omphalotropis* sp. 1, Emberton et al., 1996:210. Emberton,  
1997:1147.

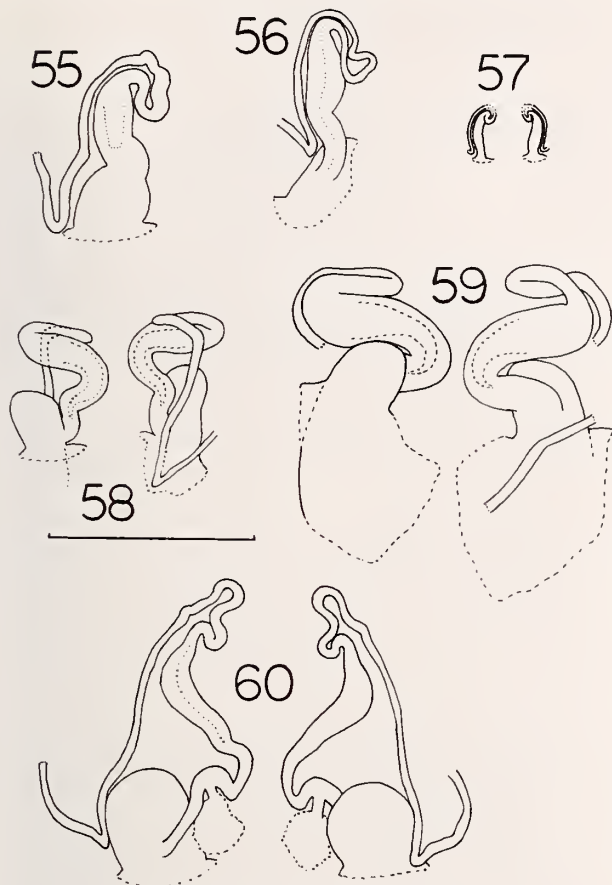
**Holotype:** USNM 860790 (ex MBI 375.01DH, adult shell).





Explanation of Figures 49–54

FPSCs of Mahermana-Ilapiry-Vasiha *Boucardicus*. Figures 49, 50. Stages in the dissection of a female to remove and clean the FPSC (demonstrated on *Boucardicus albocinctus* [Smith, 1893]). Figures 51 and (stretched and dissected open) 53. Another *Boucardicus albocinctus* (Smith, 1893), mating. Figures 52 and (stretched and dissected open) 54. *Boucardicus culminans* Fischer-Piette, Blanc, Blanc & Salvat, 1993. All scale bars 1 mm.



Explanation of Figures 55–60

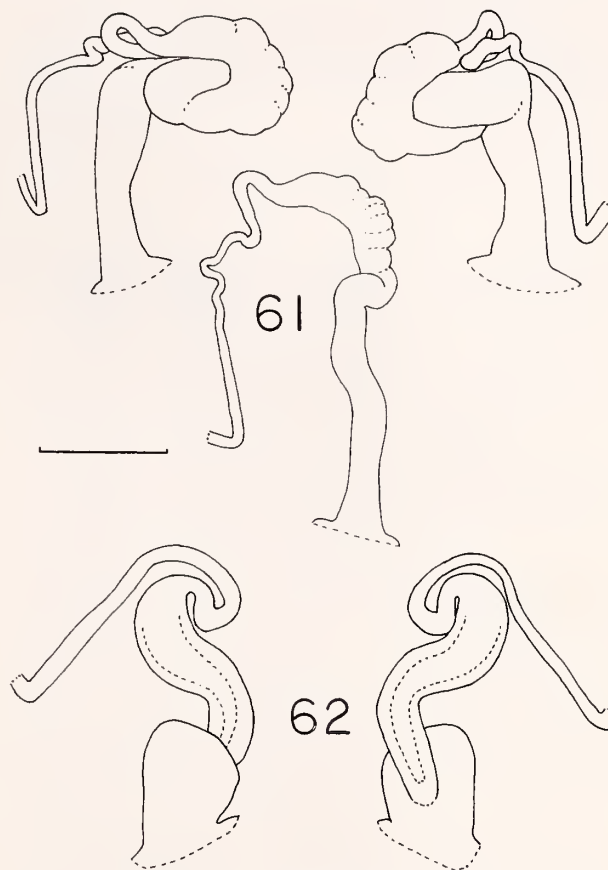
FPSCs of Mahermana-Ilapiry-Vasiha *Boucardicus*. Figure 55. *Boucardicus esetrae* Emberton & Pearce, sp. nov. Figure 56. *Boucardicus antiquus* Emberton & Pearce, sp. nov. Figure 57. *Boucardicus delicatus* Emberton & Pearce, sp. nov. Figure 58. *Boucardicus curvifolius* Emberton & Pearce, sp. nov. Figure 59. *Boucardicus victorhernandezii* Emberton, 1998. Figure 60. *Boucardicus divei* Fischer-Piette, Blanc, Blanc & Salvat, 1993. All to the same scale; scale bar 1 mm.

**Paratypes:** MBI 376.09DP (2 juv; AMS C.203435 [1 ad]), MBI 376.09AP (1 ad, 2 juv).

**Type locality:** Madagascar: Tulear Province: north of Fort Dauphin: northeast of village of Esetra: W-facing slope of Mount Mahermana, 200 m elevation: latitude 24°26'15"S, longitude 47°13'04"E: primary rainforest.

#### Description of holotype shell:

**Size and Shape.** Shell dextral. Diameter 2.6 mm; height 3.6 mm. Height-diameter ratio 1.4. Whorls 5.2. Spire angle 60 degrees. Apex angle 60 degrees. Spire profile straight. Whorl periphery rounded to slightly angular, pre-sutural ridge present. Suture depth one half whorl from aperture is 5% of shell diameter. Final umbilicus 14% of



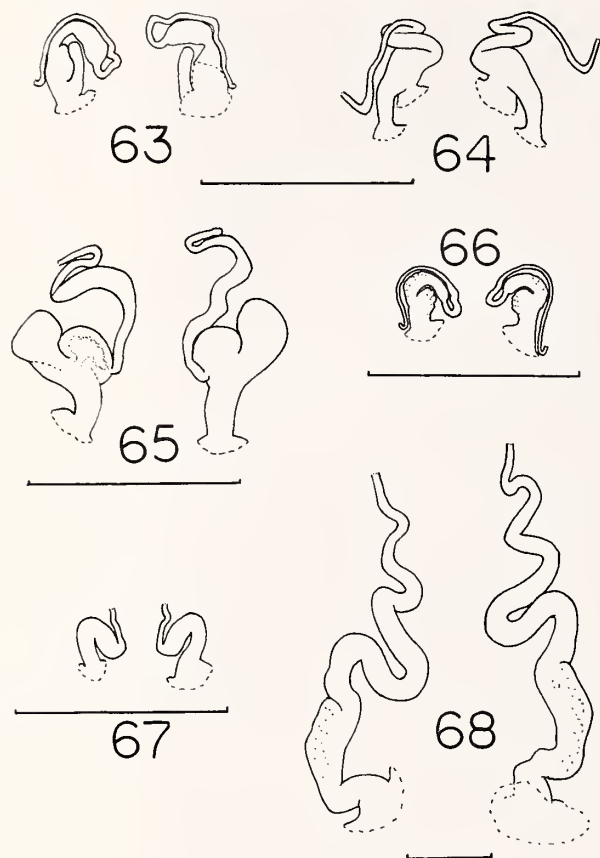
Explanation of Figures 61 and 62

FPSCs of Mahermana-Ilapiry-Vasiha *Boucardicus*. Figure 61. *Boucardicus albocinctus* (Smith, 1893). Figure 62. *Boucardicus culminans* Fischer-Piette, Blanc, Blanc & Salvat, 1993. Line drawings of same specimens photographed in Figure 35. To same scale; scale bar 1 mm.

shell diameter. Coiling tightness (whorl number divided by natural logarithm of shell diameter) 5.4.

**Aperture.** Aperture width (inside dimension, parallel to a line between the columellar and upper peristome insertions) 50% of shell diameter. Aperture height-width ratio (inside dimension, height measured to and perpendicular to a line between the columellar and upper peristome insertions) 0.85. Distance between columellar and upper peristome insertions is 54% of aperture width. Penultimate whorl projecting into body whorl. Occupying 2% of aperture height measure. Columella not truncate. Columellar plica absent. Columella slightly reflected. Apertural plane inclined downward; 15 degrees from rotational axis. Aperture shape ovate. Peristome simple; no second, internal peristome. Change in growth direction of body whorl; occurs 0.1 whorls behind aperture. Apertural dentition absent.





Explanation of Figures 63–68

FPSCs of Mahermana-Ilapiry-Vasiha *Boucardicus* and other small caenogastropods. Figure 63. *Boucardicus tridentatus* Emberton & Pearce, sp. nov. Figure 64. *Boucardicus rakotoarisoni* Emberton & Pearce, sp. nov. Figure 65. *Boucardicus mahermanae* Emberton & Pearce, sp. nov. Figure 66. *Boucardicus carylae* Emberton & Pearce, sp. nov. Figure 67. *Cyathopoma randalana* Emberton & Pearce, sp. nov. Figure 68. *Tropidophora (Ligatella) vallorzi* Fischer-Piette, Blanc, Blanc & Salvat, 1993. All scale bars 1 mm.

**Apex.** First whorl diameter 0.4 mm. First two whorls diameter 0.7 mm. Embryonic whorls smooth.

**Post-Embryonic Shell Sculpture and Color.** Post-embryonic shell with strong transverse ribs on the whorl shoulder only, lower part of whorl with extremely fine transverse rows of punctae; strong peripheral keel on the body whorl appears as a super-sutural spiral ridge on earlier whorls; another spiral ridge on the most basal part of the shell base. Basic shell color pale tan.

**Shell comparisons:** Unique within the genus for its partial, subsutural rib sculpture.

**Reproductive characters:** Unknown.

**Local distribution:** Known only from Mt. Mahermana, 100–200 m elevation.

**Etymology:** For the Vohimena Mountain Chain, north of Fort Dauphin.

*Omphalotropis costulata* Emberton & Pearce,  
sp. nov.

(Figures 25, 48)

*Omphalotropis* sp. 2, Emberton et al., 1996:210. Emberton, 1997:1147.

**Holotype:** USNM 860791 (ex MBI 381.03DH, adult shell).

**Paratypes:** MBI 378.21AP (1 ad [dissected]), MBI 379.14DP (1 juv; AMS C.203436 [1 ad]), MBI 379.14AP (1 ad), MBI 381.03DP (1 ad), MBI 381.03AP (3 ad).

**Type locality:** Madagascar: Tulear Province: north of Fort Dauphin: west of village of Mahialambo: east-south-east-facing slope of Mount Ilapiry, 200 m elevation: latitude 24°51'39"S, longitude 47°00'46"E: primary rainforest.

#### Description of holotype shell:

**Size and Shape.** Shell dextral. Diameter 2.4 mm; height 3.3 mm. Height-diameter ratio 1.4. Whorls 4.7. Spire angle 55 degrees. Apex angle 55 degrees. Spire profile straight. Whorl periphery rounded to slightly angular, pre-sutural ridge present. Suture depth one half whorl from aperture is 5% of shell diameter. Final umbilicus 14% of shell diameter. Coiling tightness (whorl number divided by natural logarithm of shell diameter) 5.4.

**Aperture.** Aperture width (inside dimension, parallel to a line between the columellar and upper peristome insertions) 53% of shell diameter. Aperture height-width ratio (inside dimension, height measured to and perpendicular to a line between the columellar and upper peristome insertions) 0.84. Distance between columellar and upper peristome insertions is 50% of aperture width. Penultimate whorl projecting into body whorl. Occupying 4% of aperture height measure. Columella not truncate. Columellar plica absent. Columella slightly reflected. Apertural plane inclined downward; 10 degrees from rotational axis. Aperture shape ovate. Peristome simple; no second, internal peristome. Change in growth direction of body whorl; occurs 0.1 whorls behind aperture. Apertural dentition absent.

**Apex.** Embryonic whorls 2.0; diameter 0.8 mm. First whorl diameter 0.5 mm. First two whorls diameter 0.8 mm. Embryonic whorls with weak transverse ribs.

**Post-Embryonic Shell Sculpture and Color.** Post-embryonic shell with strong regular transverse ribs; strong peripheral keel on the body whorl appears as a super-sutural spiral ridge on earlier whorls; another spiral ridge

on the most basal part of the shell base. Basic shell color pale yellow-orange.

**Shell variation:** No conspicuous variation in size or shape.

**Shell comparisons:** Unique in the genus for its transverse rib sculpture.

**Description of reproductive characters (MBI 378.21AP: 1 male):** Penis length 1.5 mm, 0.6 shell diameter. Penial papilla-ejaculatory-pore position dorsal. Penial dorsal papilla subterminal. Penis terminal swelling extreme, terminal-bulb width approximately 3.5 pre-bulb width. Penial gland absent. FPSC (fertilization pouch-seminal receptacle complex) unknown.

**Local distribution:** Known only from Mt. Ilapiry, 200–500 m elevation.

**Etymology:** For the sculpture of transverse ribs (*L. costulata*).

#### BOUCARDICUS CONSERVATION STATUSES

Analyses of individual species are given above in the species descriptions. To summarize, all 17 *Boucardicus* species are proposed as either Vulnerable, Endangered, or Critically Endangered. The following four species should be listed as **Critically Endangered**: *B. fidimananai* sp. nov., *B. fortistriatus* sp. nov., *B. randalanai* sp. nov., and *B. simplex* sp. nov. The 12 species that should be listed as **Endangered** are: *B. carylae* sp. nov., *B. culminans*, *B. curvifolius* sp. nov., *B. delicatus* sp. nov., *B. divei*, *B. esetrae* sp. nov., *B. magnilobatus* sp. nov., *B. maher-manae* sp. nov., *B. rakotoarisoni* sp. nov., *B. simplex* sp. nov., *B. tridentatus* sp. nov., and *B. victorhernandezi*. Two additional species qualify as **Vulnerable**: *B. albocinctus* and *B. antiquus*.

#### DISCUSSION

These descriptions of 22 small caenogastropod species support our previous distributional and ecological analyses of Mahermana-Ilapiry-Vasiha land snails (Emberton et al., 1996, 1999; Emberton, 1997). In preparation are three additional papers describing Mahermana-Ilapiry-Vasiha small pulmonates.

The DELTA system (Dallwitz et al., 1993a, b) proved useful not only in reducing the tedium and possible transcription errors involved in manually writing descriptions, but also in enforcing rigor and consistency in defining and scoring characters.

Nothing is known of the life history or autecology of any of these environmentally threatened animals.

**Acknowledgments.** We are grateful to the U.S. National Science Foundation and USAID for funding (grant DEB-9201060 to K.C.E.); to staffs of the Ranomafana National Park Project, the Madagascar Département des Eaux et Forêts, and the Tolagnaro

(Fort Dauphin) office of the World Wide Fund for Nature for logistical aid; to Roger Randalana and assistants from Esetra, Mahialambo, and Malio for collecting; to Felix Rakotomalala for curatorial assistance; and to Lucia Emberton for help in mounting the photographs.

#### LITERATURE CITED

- DALLWITZ, M. J., T. A. PAINE & E. J. ZURCHER. 1993. DELTA User's Guide: A General System for Processing Taxonomic Descriptions. 4th ed. CSIRO Information Services: Melbourne, Australia. 136 pp.
- EMBERTON, K. C. 1994. Thirty new species of Madagascan land snails. *Proceedings of the Academy of Natural Sciences of Philadelphia* 145:147–189.
- EMBERTON, K. C. 1995. Cryptic, genetically extremely divergent, polytypic, convergent, and polymorphic taxa in Madagascan *Tropidophora* (Gastropoda: Pomatiidae). *Biological Journal of the Linnean Society* 55:183–208.
- EMBERTON, K. C. 1996. Conservation priorities for forest-floor invertebrates of the southeastern half of Madagascar: evidence from two land-snail clades. *Biodiversity and Conservation* 5:729–741.
- EMBERTON, K. C. 1997. Diversities, distributions, and abundances of 80 species of minute-sized land snails in southeastern-most Madagascan rainforests, with a report that lowlands are richer than highlands in endemic and rare species. *Biodiversity and Conservation* 6:1137–1154.
- EMBERTON, K. C. 1998. *Boucardicus victorhernandezi*, a new, endangered species of cyclophorid land snail from Madagascar. *American Malacological Bulletin* 14:87–90.
- EMBERTON, K. C. In press. A survey of Madagascar's land molluscs: catalog of collections. *Molluscan Biodiversity Institute Occasional Publications* 1:1–344.
- EMBERTON, K. C., T. A. PEARCE & R. RANDALANA. 1996. Quantitatively sampling land-snail species richness in Madagascan rainforests. *Malacologia* 38:203–212.
- EMBERTON, K. C., T. A. PEARCE & R. RANDALANA. 1999. Molluscan diversity in the unconserved Vohimana and the conserved Anosy mountain chains, southeast Madagascar. *Biological Conservation* 89:183–188.
- FISCHER-PIETTE, E. & J. BEDOUCHE. 1965. Mollusques terrestres operculés de Madagascar. *Mémoires du Museum National d'Histoire Naturelle, Nouvelle Série, Série A, Zoologie* 33: 50–91.
- FISCHER-PIETTE, E., C. P. BLANC, F. BLANC & F. SALVAT. 1993. Gastéropodes terrestres prosobranches. *Faune de Madagascar* 80:1–281.
- GREEN, G. M. & R. W. SUSSMAN. 1990. Deforestation history of the eastern rain forests of Madagascar from satellite images. *Science* 248:212–215.
- IUCN. 1996. IUCN Red List of Threatened Animals. International Union for Conservation of Nature and Natural Resources: Gland, Switzerland. 368 pp.
- PANKHURST, R. J. (ed.) 1975. *Biological Identification with Computers*. Academic Press: London.
- PARTRIDGE, T. R., M. J. DALWITZ & L. WATSON. 1993. DELTA Primer: A General System for Processing Taxonomic De-



- scriptions. 4th ed. CSIRO Information Services: Melbourne, Australia. 15 pp.
- PONDER, W. F. & D. R. LINDBERG. 1997. Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. *Zoological Journal of the Linnean Society* 119: 83–265.
- SUSSMAN, R. W., G. M. GREEN & L. K. SUSSMAN. 1994. Satellite imagery, human ecology, anthropology, and deforestation in Madagascar. *Human Ecology* 22:333–354.
- VAUGHT, K. C. 1989. *A Classification of the Living Mollusca*. American Malacologists Inc.: Melbourne, Florida. 189 pp.
- WATSON, L., M. J. DALLWITZ & C. R. JOHNSTON. 1986. Grass genera of the world: 728 detailed descriptions from an automated database. *Australian Journal of Botany* 34:223–230.